

## The Mixed Dentition and Associated Skull Fragments of a Juvenile Fossil Hominid From Sterkfontein, South Africa

JACOPO MOGGI-CECCHI,<sup>1\*</sup> P.V. TOBIAS,<sup>1</sup> AND A.D. BEYNON<sup>2</sup>

<sup>1</sup>*Palaeo-Anthropology Research Group, Department of Anatomical Sciences, University of the Witwatersrand Medical School, Johannesburg, South Africa*

<sup>2</sup>*Department of Oral Biology, The Dental School, University of Newcastle upon Tyne, Newcastle upon Tyne, United Kingdom*

**KEY WORDS** dental development; Australopithecinae; juveniles; hominid evolution

**ABSTRACT** In April–May 1983, the late A.R. Hughes and his field team recovered more than 40 bone fragments and teeth from a single solution pocket of the Sterkfontein Formation. After preparation and reconstruction by JMC, it was recognised that these fragments represent a single juvenile individual (Stw 151), consisting of more than 40 cranial and dental parts, with mixed dentition. It constitutes the most complete set of jaws and teeth of an early hominid child since the Taung child was recovered in 1924. In this paper, the morphological and metrical features of the individual teeth are described. The other associated skull fragments (right ramus of the mandible, left petrous bone, right glenoid region) are also described. Comparisons are made with other South (and East) African fossil hominids. The beautiful preservation simultaneously of most of the deciduous teeth and of the permanent teeth exposed in their crypts allows an accurate analysis of the developmental sequence. A report on the dental developmental status of this juvenile is presented. On the basis of the microanatomical study of the developing permanent teeth, the estimated age at death is 5.2–5.3 years. Reconstructions of the maxillary and mandibular arcades are also offered. The morphological and metrical features of Stw 151 raise the possibility that it may represent a hominid more derived towards an early *Homo* condition than the rest of the *A. africanus* sample from Member 4. *Am J Phys Anthropol* 106:425–465, 1998.

© 1998 Wiley-Liss, Inc.

The excavation at the Sterkfontein cave deposit under the direction of P.V. Tobias, A.R. Hughes and R.J. Clarke has been operative for 30 years (Tobias and Hughes, 1969; Clarke, 1994; Tobias, 1994). During this period, the total number of entries in the catalogue of fossil hominid specimens from the site has amounted to more than 580. When added to the material recovered by Broom and Robinson during the earlier excavations at Sterkfontein, the total rises to 680 catalogued specimens.

In the Sterkfontein Formation, six Members have been distinguished (Partridge,

1978). Among these, Member 4 has yielded abundant remains of *Australopithecus africanus* but no stone artifacts, and its age has been estimated at between 2.8 and 2.6 m.y. (Partridge et al., 1991; Clarke, 1994). Some authors have suggested that more than one species of hominid may be represented in

---

Contract grant sponsor: Italian Consiglio Nazionale delle Ricerche; contract grant number AI 93.00547.04; Contract grant sponsor: South African Foundation for Research and Development.

\*Correspondence to: Dr. Jacopo Moggi-Cecchi, Istituto di Antropologia, Università di Firenze, via del Proconsolo, 12, 50122 Firenze, Italy. E-mail: jacopo@cesit1.unifi.it

Received 1 July 1993; accepted 23 March 1998.

Member 4 (Clarke, 1988; Kimbel and White, 1988; Kimbel and Rak, 1993; Calcagno et al., 1997). From Member 5, tentatively dated to between 2.0 and 1.5 m.y. (Clarke, 1994), remains assigned to early *Homo* (Hughes and Tobias, 1977) and *Australopithecus* (*Paranthropus*) *robustus* (Clarke, 1994) and stone tools have been recovered (Kuman, 1994a,b).

A more recent reassessment of the stratigraphy of Sterkfontein Member 5 has indicated that large portions of the southernmost breccia are geologically separate from the tool-bearing deposit (Kuman and Clarke, in press). These areas, where no stone tools have been found, have yielded fossil teeth of *Theropithecus oswaldi* (Kuman and Clarke, in press), and may represent a later phase of deposition than the bulk of Member 4. This later phase is tentatively dated between 2.6 and 2.0 m.y.a. (Kuman and Clarke, in press).

During April and May 1983 A.R. Hughes and his field team recovered more than 40 hominid specimens (catalogue numbers Stw 151 to 178) from partly decalcified in situ breccia in a single solution pocket in the southern part of the deposit. The exact locality of recovery was in square Aa/49 (and one specimen in square X/49) of the reference grid. The depth of recovery was between 1 m and 2.2 m below the datum line. No stone tools were found in association with these 40 specimens (Clarke, personal communication). The stratigraphic provenance was originally reported in the catalogue as "Member 4 or Member 5," since the precise relationships between the two Members in the specific area were not clear at that time.

As Stw 151 was recovered from the southern part of the deposit, in close proximity to the squares where *Theropithecus* teeth have been found, and at a relatively shallow depth, the possibility arises that Stw 151 belongs to the late Member 4 breccia deposit described by Kuman and Clarke (in press).

In July 1989, a preliminary analysis of Stw 151–Stw 178, considered with the provenance data, namely that they were found in two adjacent squares, indicated to one of us (JMC) the probability that all but three of these specimens (Stw 162, Stw 164 and Stw

169)<sup>1</sup> belonged to a single juvenile individual, now catalogued as Stw 151.

The first published reference to this juvenile specimen was in the 17th Annual Report of the Palaeo-Anthropology Research Group and Its Predecessors (Tobias, 1983), while the first tentative appraisal was in a table presented by Smith (1986). A similar table, with a short reference in the text (where the specimen is referred to as *A. africanus*), was presented by the same author in another paper (Smith, 1989). She suggested a dental age of 5 years for the specimen, on the assumption that all of the teeth that she was able to identify belonged to one juvenile individual. However, Smith did not note that all the permanent teeth (at least on one side) of the maxilla and mandible are present, some of them as fragments. Moreover, in the opinion of the present authors, some of the developmental stages that Smith assigned to individual teeth need to be slightly amended.

Other published references to this specimen are to be found in Fleagle (1988), Simpson et al. (1990, 1991), Ungar and Grine (1991), Smith (1991, 1994), Conroy and Vannier (1991a),<sup>2</sup> Moggi-Cecchi and Tobias (1993), Spoor (1993), Potente and Moggi-Cecchi (1995), and Moggi-Cecchi (1998).

The study of the developing dentition of early hominids has received much attention in recent times. For many years it was assumed that australopithecines had patterns and rates of dental development similar to those of modern humans (Mann, 1975). Different approaches to the problem have now made it evident that early hominids had distinct features of dental development, differing not only from modern humans, but also from one early hominid group to another, namely between "gracile" and "robust" australopithecines (Beynon and Dean, 1988; Conroy and Kuykendall, 1995). Other students have pointed out the enormous variability in the developmental pattern of modern human populations, so that what can be

<sup>1</sup>Stw 162 is a fragment of a left scapula of an adult individual (Berger, 1994); Stw 164 is a cranial vault fragment, very thick, most probably belonging to an adult individual; Stw 169 is a worn LI<sup>2</sup>.

<sup>2</sup>Figure 17b of Conroy and Vannier, 1991a, shows the lower incisor teeth of Stw 151. What is presented as the LI<sub>2</sub> is, in fact, the RI<sub>2</sub>.

TABLE 1. *Stw 151—list of preserved parts*

| Maxillary specimens                        | Mandibular specimens                                     | Cranial specimens                          |
|--|--|--|
| Lt maxilla with Ldm1, Ldm2, LP3, LI2 [156] | Rt body of the mandible with Rdm1, Rdm2, RM1, RP4 [153]  | petrous part Lt temporal bone [158]        |
| upper Lt dc [156]                          | lower Rt C [153]   | Rt glenoid fossa [165]                     |
| upper Lt C [156]                           | lower Lt P4, M1, base of the ramus of the mandible [158] | two occipital fragments [161a, b, c, d, e] |
| upper Lt M1 [156]                          | lower Rt I1 [152]  | two temporal fragments [161a, b, c, d, e]  |
| upper Lt I1 [155]                          | lower Lt I1 [154]  | mandibular fragments [158]                 |
| upper Rt I1 [178]                          | lower Rt I2 [176]  | root fragment [158]                        |
| upper Rt I2 [171]                          | lower Lt I2, C [177]                                     | palatal fragments [156a, b, c, d, e, f, g] |
| upper Rt dc [172]                          | lower Lt dc [151]  |  |
| upper Rt dm1 [174]                         | lower Lt dm1 [167]                                       |  |
| upper Rt dm2 [170]                         | lower Lt dm2 [166]                                       |  |
| upper Rt P3 (fragment) [173]               | lower Lt P3 [168]  |  |
| upper Rt P4 (fragment) [158]               | lower Lt M2 (fragment) [175]                             |  |
| upper Rt M1 [157]                          | Rt ramus of the mandible [163]                           |  |
| upper Lt M2 [159]                          |  |  |
| upper Rt M2 [160]                          |  |  |

Numbers in brackets are the original catalogue numbers which were given when each specimen was recovered. These numbers appear on the teeth and jaw fragments. However, the individual represented by the combined set of specimens listed above is now known as Stw 151 (Stw 151 a, maxillary; Stw 151 b, mandibular; Stw 151 c, cranial).

observed in early hominids could very well be accommodated within the range of modern human patterns of development (Mann et al., 1990, 1991).

The aims of this paper are: 1) to present a morphological and metrical description of the specimen; 2) to assess its systematic position through comparison with South African and East African early fossil hominids; and 3) to describe the stages of formation of its teeth and its dental developmental sequence in order to draw some inferences on the dental development of early hominids.

#### LIST OF PRESERVED PARTS

The specimen consists of more than 40 cranial and dental pieces. These are: 1) right body of the mandible with Rdm<sub>1</sub>, Rdm<sub>2</sub>, and RM<sub>1</sub> still in place and the rotated crown of RP<sub>4</sub> exposed in its crypt; 2) left maxillary fragment with Ldm<sup>1</sup>, Ldm<sup>2</sup>, and the developing LI<sup>2</sup> and LP<sup>3</sup> exposed in their crypts; 3) a fragment of the left body of the mandible with LI<sub>2</sub> and L<sub>C</sub> still in their relative developmental positions; 4) a fragment of the left mandibular body with LM<sub>1</sub>, the developing crown of LP<sub>4</sub> (displaced post mortem from its original position in the crypt) and part of the left ramus of the mandible; 5) right ramus of the mandible; 6) petrous part of the left temporal bone; and 7) a fragment of the right temporal bone preserving the base of the zygomatic process, the mandibular fossa, the postglenoid process, the preglenoid plane

and part of the external acoustic meatus. In addition, 23 isolated teeth (seven deciduous and 16 permanent) in different stages of development are present. Other associated cranial fragments are seven palatal fragments, two occipital fragments, two temporal fragments and eight unidentified bone fragments.

The list of parts is given in Table 1, and depicted in Figures 1 to 7. The available teeth, isolated or in the jaws, are enumerated in Table 2, together with their measurements.

On the basis of the number of teeth preserved, this is the most complete specimen of a juvenile early fossil hominid with mixed dentition recovered from South and East Africa since the discovery of the Taung child.

#### PRESERVATION AND MORPHOLOGY

##### Dental specimens

The descriptions follow Tobias (1967, 1991) and in some instances Robinson (1956) and Grine (1984, 1986). When antimeres are present, the description refers to the better preserved of the two. Measurements are in mm. Abbreviations used: IPAF = interproximal attrition facet; BL = buccolingual(ly); LL = labiolingual(ly); OC = occlusocervical(ly); IC = incisocervical(ly); MD = mesiodistal(ly); CEJ = cemento-enamel junction; CEL = cervical enamel line; DMR = distal marginal ridge; MMR = mesial marginal

TABLE 2. Available teeth of Sterkfontein juvenile, Stw 151 and their measurements

|     | Deciduous maxillary teeth |      |              |       | Deciduous mandibular teeth |              |                            |       |              |       |      |              |
|-----|---------------------------|------|--------------|-------|----------------------------|--------------|----------------------------|-------|--------------|-------|------|--------------|
|     | R                         |      | L            |       | R                          |              | L                          |       |              |       |      |              |
|     | MD                        | BL   | MD           | BL    | MD                         | BL           | MD                         | BL    |              |       |      |              |
| dc  | 6.6                       | 6.0  | 6.2          | 6.0   | —                          | —            | 6.0                        | 5.8   |              |       |      |              |
| dm1 | nd                        | 9.6  | 8.8          | 9.2   | 8.6                        | 7.2          | 8.4                        | 7.5   |              |       |      |              |
| dm2 | 9.6                       | 10.4 | 9.7          | 10.2  | 11.0                       | 9.4          | 11.1                       | 9.4   |              |       |      |              |
|     | Permanent maxillary teeth |      |              |       |                            |              | Permanent mandibular teeth |       |              |       |      |              |
|     | R                         |      |              | L     |                            |              | R                          |       |              | L     |      |              |
|     | MD                        | BL   | Crown height | MD    | BL                         | Crown height | MD                         | BL    | Crown height | MD    | BL   | Crown height |
| I1  | 9.5                       | 7.4  | 13.5         | 9.5   | 7.4                        | 13.6         | 5.8                        | 5.5   | 10.4         | 6.0   | 5.8  | 10.8         |
| I2  | 6.3                       | 6.2  | 9.2          | 6.4   | 6.1                        | nd           | 6.7                        | 6.6   | 11.6         | 6.9   | nd   | 11.7         |
| C   | —                         | —    | —            | 9.3   | 8.8                        | 13.9         | 8.5                        | 8.2   | 11.2         | nd    | nd   | 12           |
| P3  | (9.0)                     | nd   | 9.0          | (8.6) | nd                         | 9.3          | nd                         | nd    | nd           | (9.4) | 9.9  | nd           |
| P4  | nd                        | nd   | (8.6)        | —     | —                          | —            | nd                         | (9.4) | nd           | (9.6) | 10.3 | (8.5)        |
| M1  | 12.9                      | 12.9 | 6.2          | 12.9  | 13.0                       | 6.1          | 14.0                       | 11.8  | 6.7          | 13.8  | 11.7 | 6.5          |
| M2  | 13.2                      | 14.5 | 7.5          | 13.3  | 15.0                       | 7.6          | —                          | —     | —            | nd    | nd   | 6.9          |

The RP<sub>3</sub> is still in its crypt, but can be seen from an X-ray. The crown height of the RP<sub>3</sub> was measured on the lingual face; of the M<sup>1</sup> and M<sup>2</sup> on the paracone; of the M<sub>2</sub> on the entoconid; of the M<sub>1</sub> on the metaconid. — = tooth not present. nd = measure cannot be determined. MD diameters of erupted teeth have been corrected for interproximal attrition. Values in parentheses are estimates.

ridge; MLR = median lingual ridge; PR = protocone/id; PA = paracone; ME = metacone/id; HYP = hypocone/id; HYPL = hypoconulid; EN = entoconid.

#### Deciduous maxillary teeth

**Canines (Fig. 1a,b).** Both the isolated deciduous maxillary canines are intact, save that the root tip of Rd<sup>c</sup> is broken and the Ld<sup>c</sup> has a flake of enamel missing from the cusp tip. Occlusal wear is marked, with a large area of dentine exposed, sloping distally. A tiny mesial IPAF is present, lingually displaced; the distal IPAF is well developed (LL 3.9, IC 1.6). The labial face is markedly convex MD and slightly convex IC. A mesial ridge is present limiting a shallow mesiobuccal groove. A slight distobuccal groove is also evident. The CEL is curved and placed mesially to the midline. The lingual face has a strong, bulbous, basal protuberance (cingulum), skewed distally. The MMR is well developed, bounding mesially a moderately deep mesial lingual fossa. The median ridge is weakly developed. The DMR is flattened by wear and truncated distally by the distal IPAF. The CEL is curved, skewed distally. The root is subtriangular in section, with large areas of resorption on the mesiolingual face and on the distobuccal edge. The measurements at the cervix are: right MD 5.1 LL 4.7; left MD 5.2 LL 4.6.

**First molars (Fig. 1d,f,g,h).** On the isolated Rdm<sup>1</sup> the distobuccal root is missing, and a large flake of enamel is missing from the mesial and part of the occlusal surface. The Ldm<sup>1</sup> is in the maxilla and is well preserved. The occlusal wear is marked with a single, large area of dentine exposed over the PR, HYP and ME. A patch of dentine is exposed also on the tip of the PA. The mesial IPAF is located buccally to the midline and is concave and very large (BL 3.5, OC 1.6), altering the occlusal profile on its mesial border. The distal IPAF is large (BL 5.0, OC 1.7) and slightly convex. It is not possible to determine the relative dimensions of the single cusps because of the marked wear. On the occlusal surface a well-developed mesiostyle is present, separated from the PA by a deep mesial groove, moving onto the buccal face. The tip of the PA projects buccally. The buccal face is straight OC. At the base of the PA a *tuberculum molare* is present, projecting cervically. A narrow mesial buccal groove separates the PA from the mesiostyle. No V-shaped depression (Grine, 1984) is evident. The CEL is curved, following the outline of the *tuberculum molare*. On the lingual face the base of the PR is fairly rounded. On the mesiolingual edge of the PR a very faint fissure suggests the presence of a Carabelli trait. The lingual root, as observed in

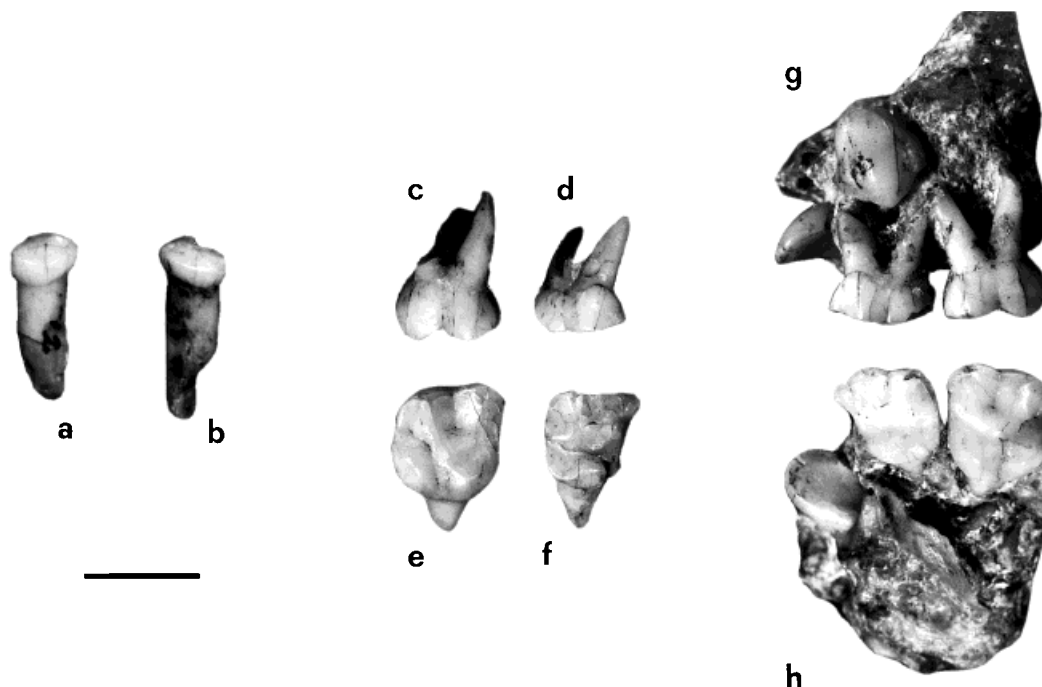


Fig. 1. Rd<sup>c</sup> (a) and Ld<sup>c</sup> (b), lingual views; Rdm<sup>2</sup>, buccal (c) and occlusal views (e); Rdm<sup>1</sup>, buccal (d) and occlusal views (f); left maxilla with Ldm<sup>1</sup>, Ldm<sup>2</sup>, LP<sup>3</sup>, LI<sup>2</sup>, buccal (g) and occlusal views (h). Scale bar = 1 cm.

the Rdm<sup>1</sup>, is oval in section, with the tip projecting lingually. The mesiobuccal root is MD compressed, with a groove on the mesial face. The root system shows clear indications of resorption. The measurements at the cervix are: right MD 7.3, BL 8.2, left MD n.d., BL 8.6.

**Second molars (Fig. 1c,e,g,h).** The crown of the isolated Rdm<sup>2</sup> is intact while the distobuccal root is missing. The Ldm<sup>2</sup> is in the maxilla and is well preserved. The occlusal wear is moderate. The PR has a subtriangular pit of exposed dentine. A tiny pit of dentine is present also on the tip of the PA. ME and HYP show marked wear facets. The mesial IPAF is large (BL 4.9, OC 1.7) and slightly concave. The distal IPAF is oval (BL 4.5, OC 3.1), slightly convex and is placed lingual to the midline. The PR is the largest cusp, while PA, ME and HYP are smaller and similar in size. A large and shallow central fossa is evident, from which departs a pronounced buccal groove. A well-developed trigon crest is present, although re-

duced by wear. The deep distal fovea is bounded by a thick DMR. From the distal fovea a well-incised oblique fissure extends lingually. The buccal face is slightly convex OC, and a buccal groove separates PA from ME. The CEL is straight. The cusp tip of the ME projects occlusally. The lingual face is convex at its base and shows a deep distal-buccal groove separating the HYP and the PR. On the mesiolingual corner a short fissure, extending towards the occlusal surface, indicates the presence of a Carabelli feature. The CEL slopes cervically at the level of the IP. On the Rdm<sup>2</sup> the mesiobuccal root is MD compressed, with grooves on both faces. The thick lingual root, oval in section, projects lingually. Clear indications of resorption are present on both roots. The measurements at the cervix are: right MD 7.8, BL 10.1; left MD n.d., BL 9.9.

#### Deciduous mandibular teeth

**Canine (Fig. 4e).** Only the isolated Ld<sup>c</sup> is present. The root tip is broken; a chip of root is missing from the distolingual surface,



near the CEJ. A flake of enamel is missing from the mesial edge of the crown. A large wear facet with dentine exposed (MD 2.8, LL 1.3), oval in shape, is evident on the cusp tip, and it slopes distally. A mesial IPAF is not present. A large distal IPAF is evident on the distobuccal edge of the buccal face (LL 3.0, IC 2.8). The lingual face has a well-developed, lingual cingulum skewed distally to the midline, giving rise to a tiny lingual tubercle. A large, rounded median ridge is present. The MMR, although quite worn, is thick and low. Distal to it, a shallow mesial lingual fossa is present. The DMR is short and thick and with the median ridge delimits a deep distal fossa. The CEL is curved, bounding the cingulum. The buccal face is markedly convex MD and almost straight IC. There is no cervical prominence. The CEL is almost straight. The root is subtriangular in section with faint grooves on the mesiolingual and distolingual faces, near the apex. A large area of resorption is evident in the mid-part of the mesiolingual face. The measurements at the cervix are: MD 5.1, LL 5.4.

**First molars (Fig. 4a,b,h,i).** The isolated Ldm<sub>1</sub> has a well-preserved crown and the roots, on the lingual side, are broken just below the CEJ. On the buccal side 5.1 mm of the mesial root and 6.1 mm of the distal root are preserved. The Rdm<sub>1</sub> is in the mandible and overall is well preserved. The occlusal wear is marked, with large oval areas of dentine exposed on the PR (MD 3.2, BL 2.4) and the HYP (MD 3.4, BL 3.4). Tiny patches of dentine are present on the cusp tip of the ME and on the EN. The mesial IPAF is large and almost circular (BL 2.7, OC 2.7) and concave. It is placed buccally to the midline. The large distal IPAF, as evident on the Ldm<sub>1</sub>, is oval in shape and flat (BL 4.7, OC 1.9). The occlusal outline is trapezoidal, with a prominent mesiobuccal extension. The marked wear obscures many morphological details. The four main cusps are evident, with the PR as the largest, ME and HYP approximately the same size and EN the smallest. The PR is mesially placed to the ME. The ME cusp tip is markedly projecting buccally. The MMR although worn is thick and low. A deep, Y-shaped mesial fo-

vea, is present, lingual to the midline. The central fossa is broad and shallow, and the lingual groove is evident. On the buccal face a marked *tuberculum molare* is present at the base of the PR. A short but moderately deep mesiobuccal groove crosses obliquely the mesial side of the PR. A moderately deep principal buccal groove is present. The buccal portion of the HYP is convex both OC and MD. The CEL curves around the *tuberculum molare*, becoming horizontal distally. The lingual face is markedly convex OC and moderately convex MD. The CEL is almost straight, with a slight cervical extension at its midpoint. Part of the root system can partly be observed on the Ldm<sub>1</sub>. Both roots are thick and with indications of resorption. The mesial root is elliptical in section and MD compressed. The distal root is oval. The measurements at the cervix are: right MD 7.6, BL 5.3; left MD 7.4, BL 6.3.

**Second molars (Fig. 4c,d,h,i).** The isolated Ldm<sub>2</sub> is well preserved; only the tips of the mesial roots are broken. The Rdm<sub>2</sub> is in the mandible. It has a chip of enamel missing from the HYP. Occlusal wear is moderate. The PR has a large basin of dentine exposure (MD 3.2, BL 3.8), oval in shape, merging distally with a similar basin on the HYP (MD 3.5, BL 2.5). A small pit of dentine is evident on the HYPL. Large wear facets are present on the ME and the EN. The mesial IPAF is oval in shape (BL 4.7, OC 2.3) and somewhat concave both BL and OC. The distal IPAF is oval (BL 4.8, OC 2.9) and flat. The occlusal outline is rectangular, but rounded buccally. The ME is the largest cusp, followed by PR, IP, EN and HYPL in decreasing order of size. The PR is mesially placed to the ME. A marked fissure suggests the existence of a short deep mesial fovea. Distal to it, a deep pit marks the remain of the mesial fissure. This morphology appears similar to what Grine (1984) describes as "a 'doubled' anterior fovea, in that a mesial and distal fossid are separated by a narrow accessory enamel ridge" (Grine, 1984, p. 826). The central fossa is broad and shallow; the lingual groove is evident. A small, deep, distal fovea is bounded by a short and thick DMR. The buccal face is convex both MD and OC. A well-developed, thick, enamel

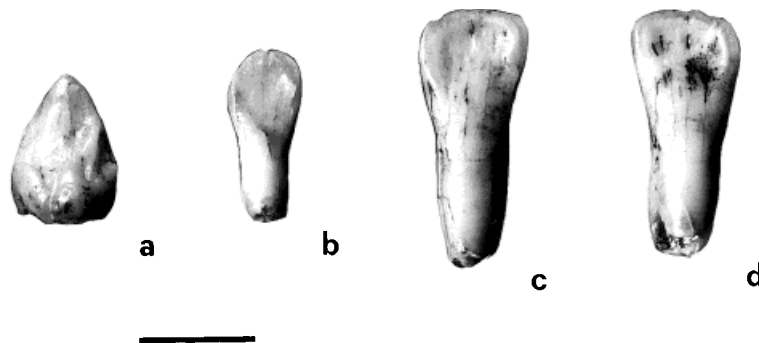


Fig. 2.  $RI^2$  (a),  $RI^1$  (b),  $LI^1$  (c),  $LI^2$  (d), lingual views. Scale bar = 1 cm.

shelf is present at the base of the mesial buccal groove; it is incised at its mesial end by a faint fissure. The CEL is horizontal. The lingual face is slightly convex OC and MD. The lingual groove is weak. The CEL is straight, extending slightly cervically in its midpart. The roots, as observed on the  $Ldm_2$ , are flattened, with the mesial root compressed MD along its central part. The buccal portion of the distal root projects both buccally and distally. Marked resorption is present on the distal root. The measurements at the cervix are: right MD 9.9 BL 8.0; left MD 9.1 BL 8.4.

#### Permanent maxillary teeth

**Central incisors (Fig. 2c,d).** Both the isolated maxillary central incisors are present and well preserved. Wear is very slight. An IPAF is present on the mesial surface (IC 2.1, LL 1.1) and tiny facets are evident on the lingual side of the incisal margin. The labial face has a trapezoidal outline. The mesial corner is angulated, the distal more rounded. The incisal edge has three mamelons of different size (four on the  $LI^1$ ). Faint vertical grooves cross the incisal third of the crown. The CEL is straight mesially, and it moves cervically in the distal half of the face. The lingual face is markedly concave in the incisal third, both MD and IC. The gingival eminence is marked, but no tubercle is present. The MMR is faint; the DMR is well developed, thick and low. A fairly marked central ridge is evident, sloping down into a moderately deep lingual fossa. The CEL is horizontal. The measurements at the cervix are: right MD 6.3, LL 7.2; left MD 6.4, LL

7.2. The root cross-section is subtriangular with vertical grooves on both the mesial and the distal surfaces. The root lengths, measured on the buccal side, are 8.9 mm in  $LI^1$ , and 9.8 mm in  $RI^1$ .

**Lateral incisors (Fig. 1g,h; Fig. 2b).** The  $RI^2$  is isolated. The  $LI^2$  is in the maxilla, and it has probably been displaced post mortem. A small flake of dentine is missing from the labial face of the developing root of  $RI^2$ . Both teeth were unerupted. The  $LI^2$  can be seen as emerging through the bone. The labial surface, oval in outline, is convex both MD and IC. The mesial and the distal portions of the incisal edge are both markedly rounded, the distal more so, resulting in a well-rounded profile of the crown. A notch is present on the midpart of the incisal edge. The lingual surface is somewhat concave both MD and IC. The MMR is moderately thick and low. The DMR is very thick and high. The MMR and the DMR merge cervically into a strongly developed gingival eminence with a tiny lingual tubercle distal to the midline. The lingual fossa is broad and fairly deep. Shovelling is slightly marked. A moderately expressed incisal ridge (sensu Robinson, 1956) is present, cut in its midpart by a short, vertical groove. The CEL is straight. The measurements at the cervix are: right MD 4.5, LL 6.0. The developing root of  $RI^2$  is oval in outline, and strongly compressed MD. Faint grooves are evident both on the mesial and the distal face. The developing root of the maxillary  $RI^2$  is 6.0 mm long.

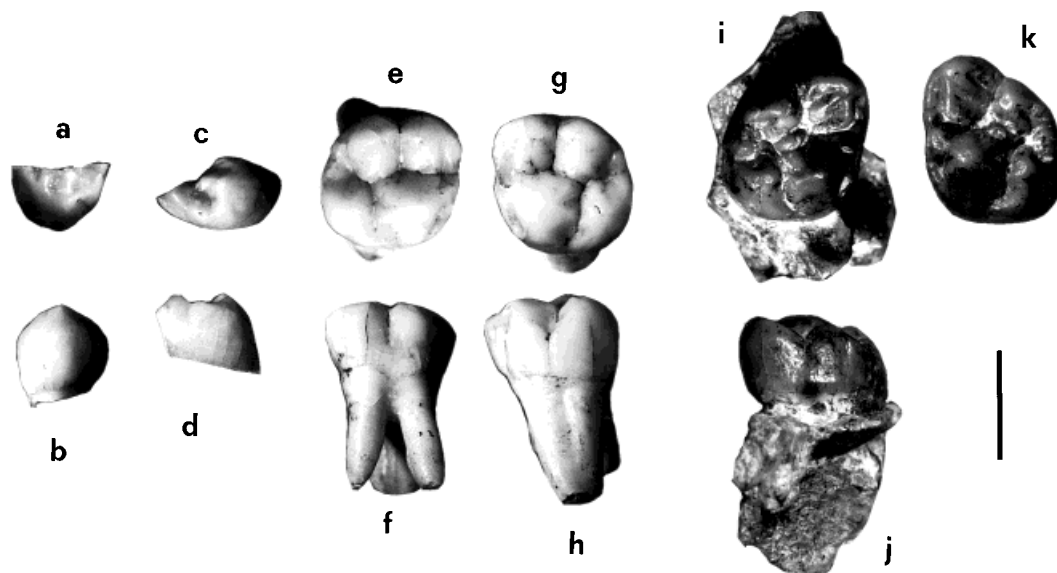


Fig. 3. RP<sup>3</sup> (fragment), occlusal (a) and lingual views (b); RP<sup>4</sup> (fragment), occlusal (c) and mesial views (d); RM<sup>1</sup>, occlusal (e) and buccal views (f); LM<sup>1</sup>, occlusal (g) and lingual views (h); RM<sup>2</sup>, occlusal (i) and buccal views (j); k: LM<sup>2</sup>, occlusal view. Scale bar = 1 cm.

**Canine (Fig. 2a).** The isolated L<sup>C</sup> is present and well preserved, apart from tiny chips of enamel missing from the labial side at the CEJ. The tooth was not erupted. The labial face is pentagonoid in outline, convex IC and, more so, MD. The cusp is high with its axis along the midline; the mesial and distal edges are both very steep. A distinct MMR is present; the DMR is weakly expressed. The lingual face is slightly concave IC. The MMR is strongly developed, thick and high, interrupted by a notch near the mesial edge. Mesial to the midline a marked ridge crosses the face from the base of the MMR to the cusp tip. A marked lingual tubercle is present, giving rise to a short and thick ridge, whose apex turns distally merging into a strongly developed distal accessory ridge. A broad, short DMR is also evident, with a tiny cuspule on its edge, near the lingual tubercle. On the mesial and on the distal face some 1.8 mm of the developing root can be observed; no root development is evident on the lingual face. The measurements at the cervix are: MD 7.8, LL 8.4.

**Third premolars (Fig. 1g; Fig. 3a,b).**

The developing LP<sup>3</sup> is in the maxilla and is well preserved. Only the lingual half of the crown of RP<sup>3</sup> is preserved. The buccal face (as evident on the LP<sup>3</sup>) becomes narrow towards the cervix. It is markedly convex both MD and OC, with the apex of the MD convexity skewed mesially to the midline. The buccal cusp is high, with steep mesial and distal edges. Faint buccal grooves are evident. The lingual face on the RP<sup>3</sup> is very convex MD and slightly convex OC. The cusp tip is mesial to the midline. The CEL is curved distally. The lingual portion of the occlusal surface (on the RP<sup>3</sup>) has four thick, rounded cusp ridges, moving down mesially and distally from the cusp tip. Some 2 mm of the developing root can be observed on the distal face of RP<sup>3</sup>.

**Fourth premolar (Fig. 3c,d).**

The crown of the RP<sup>4</sup> is represented by a fragment showing the buccal cusp and part of the lingual cusp. In occlusal view, an additional cuspule is evident on the MMR. From the buccal cusp tip, strong enamel ridges slope



mesially and distally. On the buccal face the high cusp is evident, with mesial and distal steep edges.

**First molars (Fig. 3e,f,g,h).** Both first maxillary molars are present as isolated teeth. The RM<sup>1</sup> is very well preserved. The LM<sup>1</sup> has the mesiobuccal root tip broken and a small portion of the base of the distobuccal root is missing. Small facets of occlusal attrition are present on all the cusps. A slightly concave, oval, mesial IPAF (BL 4.5, OC 3.1) is evident. The occlusal outline is a rounded parallelogram with the HYP bulging both distally and lingually. The buccal cusps are placed mesially to the lingual ones. The four main cusps are well developed, with the PR as the largest and the three others smaller and of approximately the same size. The MMR is marked and thick and it delimits a fairly large and deep mesial fovea bounded distally by an interrupted mesial crest. The central fovea is deep and broad and deeply incised buccal, mesial and distal fissures depart from it. The trigon crest (*crista obliqua*) is well developed although it is cut by the distal fissure. A deep oblique fissure is evident, merging with a distal fissure and sloping down into a wide and deep distal fovea. The DMR is thick and low with two faint notches on its buccal edge, suggesting the existence of a slightly developed distal marginal conule (distostyle sensu Grine, 1984). The buccal face is almost straight OC, with a faint basal prominence. The buccal groove is deep and narrow. A small parastyle (sensu Robinson, 1956) is present. The CEL is straight, extending cervically at the level of the root bifurcation. The lingual face is convex both MD and OC. The basal eminence is fairly marked. On the mesiolingual corner a Carabelli trait is present as a marked V-shaped furrow with a tiny cuspule on the lingual branch of the V. The lingual groove is deeply incised. At its end, in the central part of the face, two enamel ridges (parastyles of Tobias, 1991) arise, one towards the tip of the PR, and the other towards the tip of the HYP. The CEL is horizontal. The buccal roots are oval in outline, with strongly compressed MD dimensions. The lingual root has an irregular

conical shape, with a slight MD compression and it projects both lingually and distally. A marked longitudinal groove is present on its lingual side. The root lengths are: right mesio-buccal 11.2, disto-buccal 10.3, lingual 11.2; left disto-buccal 10.9, lingual 10.8. The measurements at the cervix are: right MD 10.2, BL 12.6; left MD 10.3, BL 12.5.

**Second molars (Fig. 3i,j,k).** Both the isolated, unerupted RM<sup>2</sup> and LM<sup>2</sup> crowns are present and well preserved. Only a flake of enamel is missing at the base of the PR on the mesiolingual corner of LM<sup>2</sup>. The occlusal outline is oval, with the main cusps evident, although the distal part is markedly reduced. The buccal cusps are placed strongly mesially to the lingual ones. The PR is the largest cusp, followed by PA, HYP and ME. The MMR is thin and it has a small mesioconule on its midpoint. The mesial fovea is fairly deep and elongated and it extends buccally. The lingual portion of the MMR is occupied by a well-delineated cuspule (epiconule, Grine, 1984). Two thick cusp ridges flow from the tip of the PA into the broad and shallow central fossa; of the two, the mesial one represents the paraconal portion of the protocone-paracone crest (mesial crest), which lacks the protoconal counterpart. Fairly marked buccal, mesial and distal fissures run from the central fossa. A groove, parallel to the distal fissure cuts the weak trigon crest, thus helping delimit a well-developed metaconule. A thick ridge moves from the tip of the HYP into the deep distal fovea. The latter is bounded by a DMR which is occupied by a well-developed distoconule subdivided into two cuspules of different size. A well-delineated distostyle is also present. From the distal fovea a deep oblique fissure moves onto the lingual face. The buccal face is straight OC with a moderately developed basal eminence. The buccal groove and a small distal buccal groove on the ME are both marked. The CEL is straight. The lingual face is convex both OC and MD. No basal eminence is evident. On the mesiolingual corner of the PR a large, deep, V-shaped furrow represents the Carabelli trait. A faint protoconal cingulum is also present. The lingual groove is marked

and it is bounded distally by a thick curved enamel ridge. The CEL is straight. The measurements at the cervix are: right MD 10.2, BL 13.8; left MD 10.6, BL 13.7.

#### Permanent mandibular teeth

**Central incisors (Fig. 5a,b).** The RI<sub>1</sub> and LI<sub>1</sub> are present as isolated teeth and are well preserved. A small flake of dentine is missing from the labial face of the developing root of LI<sub>1</sub>. A tiny interproximal attrition facet is present on the mesial surface (right IC 2.8, LL 1.3). Interestingly, the mesial interproximal wear facets do not lie squarely on the mesial surfaces of the teeth: that of the LI<sub>1</sub> is placed on the mesiolingual margin, while that of the RI<sub>1</sub> is placed on the mesiolabial margin. This asymmetry suggests some crowding of the mandibular central incisors, the left having overlapped the right. Slight attrition facets are present on the labial side of the incisal margin. This indicates that a small degree of overbite was present, rather than an edge-to-edge contact. The labial face has a triangular outline and is slightly convex IC and almost straight MD. The incisal edge has slightly rounded corners, and five mammellons, of different size, are present. The CEL is V-shaped. The lingual face is concave IC and flat MD. There is no gingival eminence. The MMR and the DMR are faintly expressed. From the central mammellon a thin, faint enamel ridge moves down as far as the central part of the face. The measurements at the cervix are: right MD 4.0, LL 5.4; left MD 4.1, LL 5.7. The root outline is oval, and strongly compressed MD. The developing roots as measured on the buccal face are 8.8 mm in RI<sub>1</sub> and 8.0 mm in LI<sub>1</sub>.

**Lateral incisor (Fig. 5c,e).** The LI<sub>2</sub> is in a fragment of the mandible with the L<sub>C</sub>, and it is well preserved. The RI<sub>2</sub> is isolated. Only a small flake of dentine is missing from the mesiolingual face of the developing root of RI<sub>2</sub>. Both these teeth were unerupted. The LI<sub>2</sub> can be seen as emerging through the bone. The labial face has an irregular, asymmetrical, oval outline. The surface is slightly convex MD and IC. The incisal edge has the distal corner markedly rounded, while the mesial one is more angulated. Four mamel-

ons of different size are present on the edge. On the distal corner, a very markedly expressed mamelon is apparent. A weakly expressed MMR can be observed. The CEL is curved. The lingual face is concave IC and a moderately marked gingival eminence can be observed. There is no MMR. A low but well-developed DMR is present. A thin, faint central enamel ridge is evident just below the incisal edge. The measurements at the cervix are: MD 4.4, BL 6.5. The outline of the root is oval and MD compressed. An incipient longitudinal groove can be observed on the distal face. The RI<sub>2</sub> root measures 5.5 mm.

**Canines (Fig. 5d,f).** Both L<sub>C</sub> in a fragment of mandible and the isolated R<sub>C</sub>, are present. A small flake of enamel is missing from the labial aspect of the crown of the R<sub>C</sub> at the CEJ. The L<sub>C</sub> is well preserved. The labial face has an asymmetrical pentagonoid outline and is extremely convex both IC and MD. The cusp tip is high and sharp. A thin but marked MMR is present as is a fairly well-developed DMR ending in a tiny but distinct cuspid. The lingual face is concave IC. The gingival eminence is marked, but there is no canine tubercle. The MMR is broad and low with a thin edge. A weak mesial groove is evident. The DMR is well developed, with a thin edge. A strong, broad and low, lingual ridge, is evident; its distal portion has a sharp, high edge. The distal edge of the lingual ridge and the DMR delimit a deep, V-shaped distal groove. The MMR, DMR and the lingual ridge merge at the level of the gingival eminence. The measurements at the cervix are: MD 6.5, LL 6.4.

**Third premolar (Fig. 4n,o).** The isolated crown of the LP<sub>3</sub> is present, and a flake of enamel is missing from its mesial portion near the crown base. In occlusal view the crown has an irregularly oval shape, with a marked distolingual extension. Both cusps are evident and well developed, with the lingual cusp mesially placed to the central protoconid ridge. The buccal cusp is larger and higher than the lingual. The mesial fovea is broad and deep and it is bounded buccally by a well-developed marginal process and distally by a transverse crest run-

ning from the tip of the buccal cusp to the base of the lingual cusp, where a marked, uninterrupted, central longitudinal fissure is evident. The distal fovea is moderately deep and large. The distal wall of the distal fovea is occupied by a well-developed talonid, where three distinct cusplids of different sizes are evident. The buccal face is convex both MD and OC. A distinct distal buccal groove is present. The upper portion of the mesial buccal groove is evident. The lingual face has a marked prominence in its distal portion, making the surface unevenly convex both MD and, less so, OC. A faint distal lingual groove is present. The talonid length is 3.3.

**Fourth premolars (Fig. 4f,g,i).** Both  $P_4$ s are in their crypts in the mandible. Their crowns are well preserved. In occlusal view (as evident on the  $LP_4$ ), the buccal cusp is larger than the lingual cusp. The cusps are subequal in height, with the lingual cusp mesial to the buccal. The MMR is thick and low, incised by a notch in its midpart. The mesial fovea is moderately deep and it is closed distally by a continuous transverse crest. The central longitudinal fissure is deep and uninterrupted. The distal fovea is broad and deep. The talonid has four cusplids, very thick and low, and of different sizes. The buccal face is convex OC and MD, with the apex of the MD convexity at the level of the buccal cusp. A well-marked, curved, mesial buccal groove is evident. The distal buccal groove can also be observed, incising the occlusal margin and delineating the disto-buccal cusplid of the talonid. The lingual face is markedly convex both OC and MD. The talonid length is 3.6.

**First molars (Fig. 4f,h,i,j,k).** Both first permanent molars are present. The  $RM_1$  is in the mandible, the  $LM_1$  is in a fragment of the mandible. In each of the  $LM_1$  and the  $RM_1$  the disto-buccal root tip is broken. Distinct, small facets of occlusal attrition are present on the main cusps. The mesial IPAF (as evident on the  $LM_1$ ) is oval in shape and slightly concave (BL 4.8, OC 2.8). The occlusal outline is oval, with a slight disto-buccal projection. The ME is the largest cusp, although similar in size to the

smaller PR; the HYP is the next smaller, followed by HYPL and EN, of approximately the same size. The primary fissure pattern shows the buccal and the lingual grooves almost along the same BL plane, with a ME-HYP contact. No MMR can be observed because of wear, but the mesial fovea is completely occupied by two small mesioconulids, evidently sloping from the MMR. The central fossa is broad and shallow and from it deep and narrow mesial, distal, buccal and lingual grooves originate. A well-developed *tuberculum intermedium* is evident reaching up to the central fossa. The distal fovea is small and deep, bounded by a thin and low DMR, which is incised by a notch in its central portion. The buccal face is fairly convex MD, less so OC. The deep mesial buccal groove ends in a well-developed enamel shelf, which, on the  $RM_1$ , is incised on its mesial end. The CEL, as evident on the  $RM_1$ , is horizontal, with a slight extension at the level of the root bifurcation. On the distobuccal corner, just below the tip of the HYPL, a tiny, distinct tubercle is evident. This is delineated by a marked groove which originates from the distal buccal groove, passes onto the HYPL, where it curves distally. The lingual face is almost straight both OC and MD. Two parallel, deep, lingual grooves, limit mesially and distally the *tuberculum intermedium*. The CEL is horizontal. Parts of the root system can be observed on each  $M_1$ . The roots are thick and the distal root is elongated BL, with a disto-buccal projection on the  $LM_1$ . The root lengths are: right distal 11.9; left distal 11.6. The measurements at the cervix are: right MD 11.9, BL 11.1; left MD 11.6, BL n.d.

**Second molar (Fig. 4l,m).** Only the distolingual half of the crown of  $LM_2$  is present and well preserved. The EN, HYPL and part of the distal slope of the ME are evident. Mesial to the EN a marked lingual groove is present. The distal fovea is fairly large and deep. The thin DMR has in its midpart a well-developed *tuberculum sextum*. On the distal face, just below the tip of the IPL, a faint groove is evident. The lingual face is slightly convex both OC and MD, with a marked lingual groove.

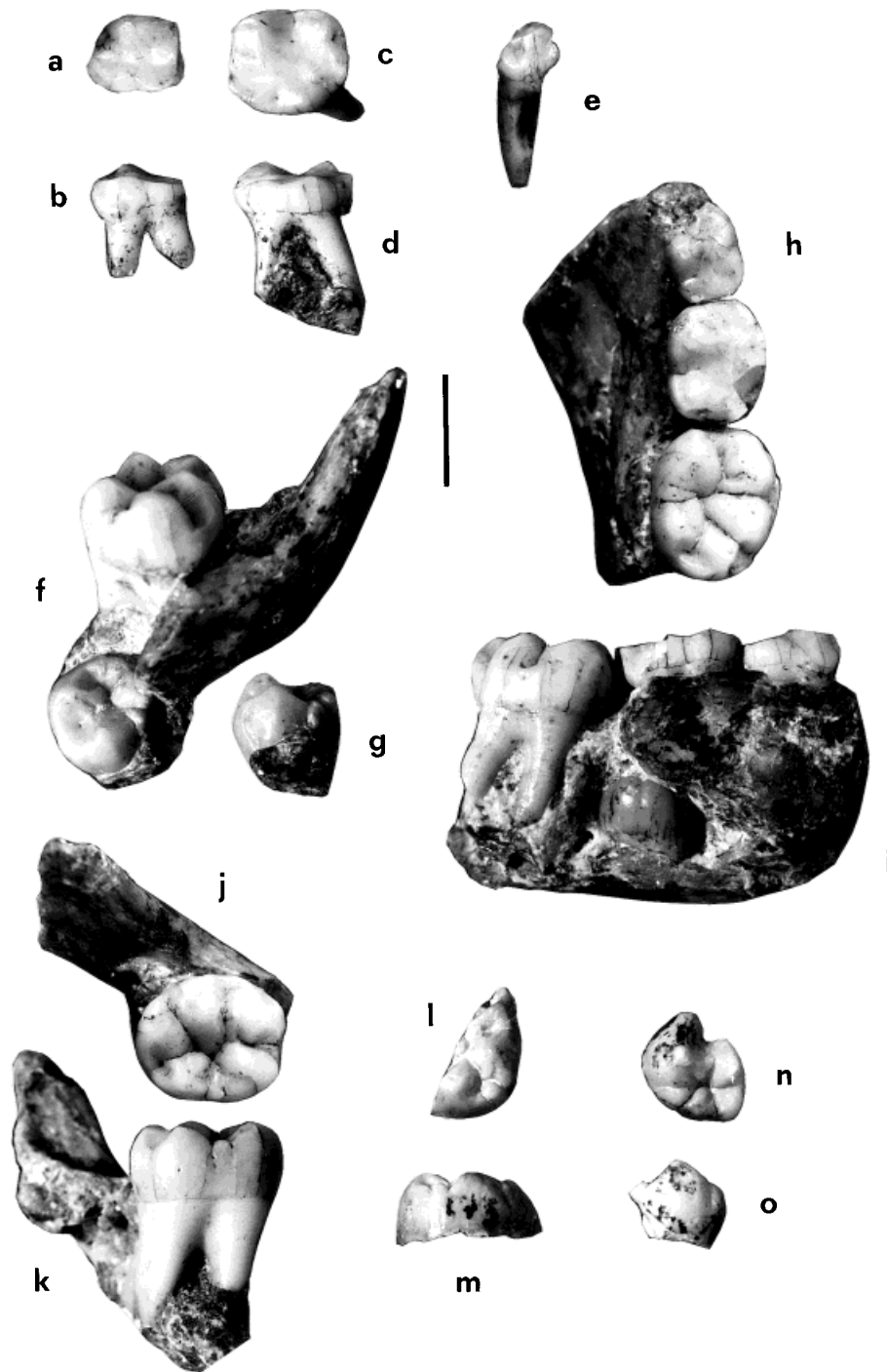


Fig. 4. Ldm<sub>1</sub>, occlusal (a) and buccal views (b); Ldm<sub>2</sub>, occlusal (c) and buccal views (d); Ld<sub>1</sub>, lingual view (e); f: base of the left ramus of the mandible with LM<sub>1</sub>, and (in occlusal view) displaced LP<sub>4</sub>; g: LP<sub>4</sub>, buccal view; right body of the mandible with Rdm<sub>1</sub>, Rdm<sub>2</sub>, RM<sub>1</sub>, RP<sub>4</sub>, occlusal (h) and buccal views (i); LM<sub>1</sub>, occlusal (j) and lingual views (k); LM<sub>2</sub> (fragment), occlusal (l) and distolingual views (m); LP<sub>3</sub> (fragment), occlusal (n) and buccal views (o). Scale bar = 1 cm.



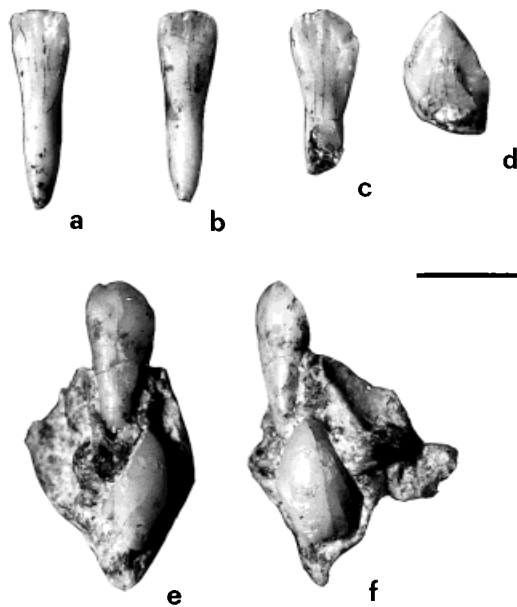


Fig. 5. LI<sub>1</sub> (a), RI<sub>1</sub> (b), RI<sub>2</sub> (c), RC (d), lingual views. e: Buccal view of LI<sub>2</sub>. f: buccal view of LC. Scale bar = 1 cm.

#### Other cranial pieces

The descriptions follow the terminology of Tobias (1967, 1991) and Weidenreich (1936, 1943).

**Right ramus of the mandible (Fig. 6c,d,e).** A well-preserved right ramus of the mandible is present except for the gonial angle. The medial portion of the condyle is heavily abraded. The condyle in superior view is elliptical and compressed anteroposteriorly. Its axis is posteromedially oriented, close to the coronal plane. In lateral view, the ramus is broad (35 mm, as measured). Below the condyle a moderately developed *crista ectocondyloidea* passes inferiorly and anteriorly into a prominent *eminencia lateralis rami*. A depression anterior to the lateral eminence is evident. The mandibular notch is moderately deep (7 mm—no. 70/3 of Martin and Knussmann, 1988) and wide. The condyle and the coronoid process are at the same level. The distance from the tip of the coronoid to the top of the condyle is 26 mm. Below the rounded coronoid process a slight *incisura subcoronoidea* (emphasized by some

bone exfoliation) is evident. Moderate buttressing is present in the area of the coronoid. On the medial face, the most relevant feature is a massive *torus triangularis rami*, which gives rise to a strongly developed, thick *crista endocoronoidea*, passing superiorly and anteriorly towards the coronoid process. A very faint *crista endocondyloidea* is present. A large *planum triangulare* is evident, with a broad hollow in its anterior portion. The *crista endocoronoidea* together with the edge of the ramus delimits a deep and concave *recessus mandibulae*. Although abraded the medial portion of the condyle is well developed, extending for some 8 mm supero-inferiorly. A large *foramen mandibulare* is present (at its opening about 5 mm long antero-posteriorly), with a notable bony lip as its anterior margin. From it a distinct but narrow mylohyoid groove passes inferiorly and anteriorly. At the posterior edge of the ramus, at the level of the mandibular foramen, a remarkably strong *tuberculum pterygoideum inferius* is present. In anterior view, the thick anterior edge of the ramus flares laterally at the coronoid apex. The exposed internal part of the ramus shows the posterior surfaces of the crypts of the developing RM<sub>3</sub> and, below it, RM<sub>2</sub>. Below this, the sectioned mandibular canal is evident. In posterior view, the posterior edge shows some degree of inversion. The condyle is well developed. Its axis is infero-medially orientated. The condylar neck is thick and short.

**Right temporal bone fragment (Fig. 6a,b).** A fragment of the right temporal bone is present, preserving the base of the zygomatic process, part of the squamous surface, the mandibular fossa, the postglenoid process, the preglenoid plane and the lateral portion of the external acoustic meatus. The fragment was originally broken into two matching parts (now glued back) along a crack running mediolaterally from the lateral margin of the articular eminence, through the mandibular fossa, to its posterior wall, at the base of the postglenoid process. The posterior surface of the external acoustic meatus is broken at the level of the base of the mastoid process.



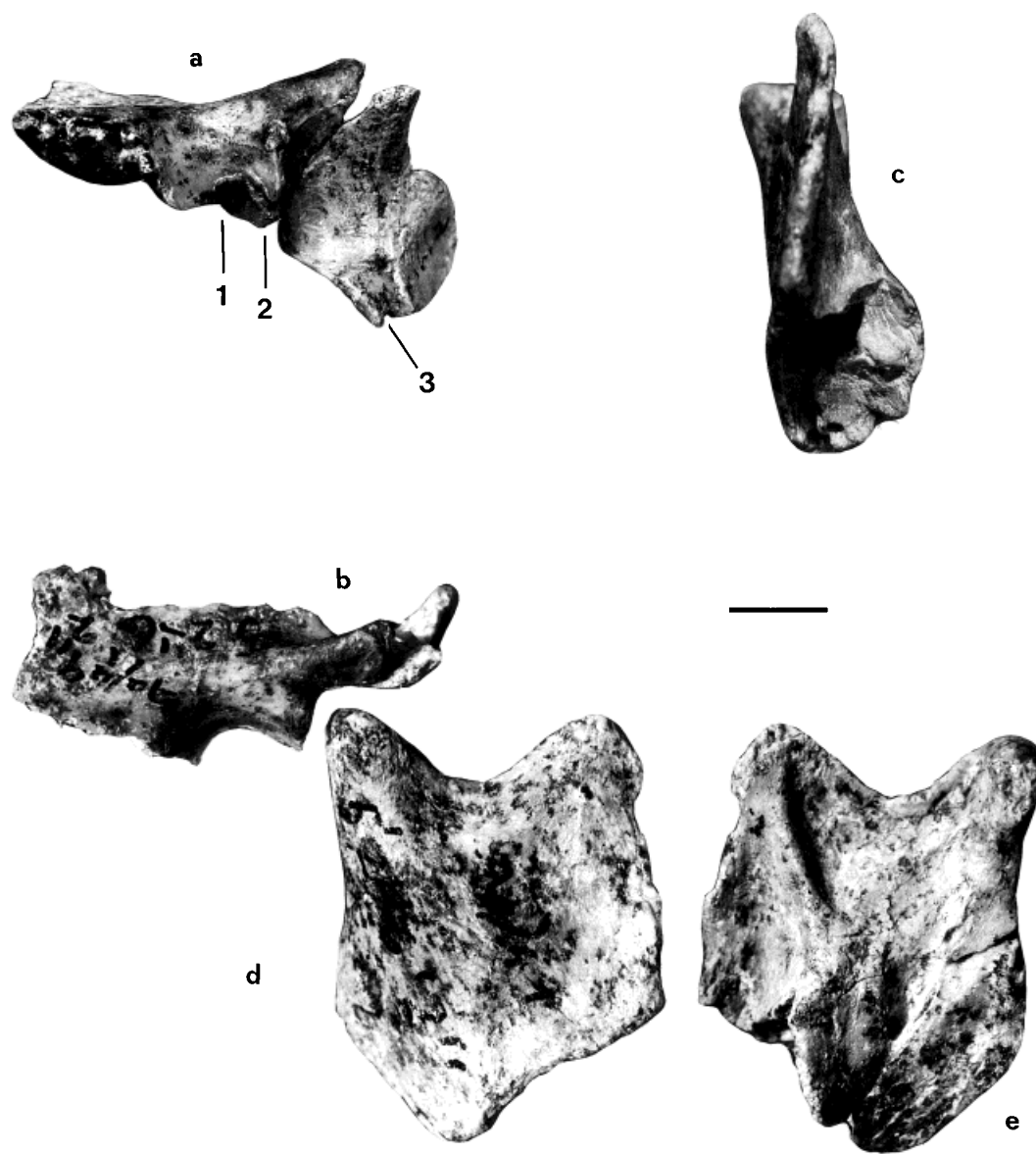


Fig. 6. Right temporal bone fragment, inferior (a) and lateral views (b). 1 = external acoustic meatus; 2 = postglenoid process; 3 = foramen spinosum. Right ramus of the mandible, anterior (c) lateral (d) and medial (e) views. Scale bar = 1 cm.

In lateral view, the bone surface above the external acoustic meatus is smooth, with no indication of a suprameatal crest. The preserved portion of the external acoustic meatus shows a parabolic outline and a smooth surface. On its anterior surface, lying on the back of the postglenoid process, a roughened area of bone delineates the developing tym-

panic plate. The postglenoid process, markedly projecting, is subtriangular in sagittal section, with a thin and sharp edge, and its depth (following Tobias, 1991) is about 6.5 mm (8 mm following no. 85 of Wood, 1991a). Its anterior profile is symmetrically curved. The distance between the broken edge of the posterior surface of the external acoustic

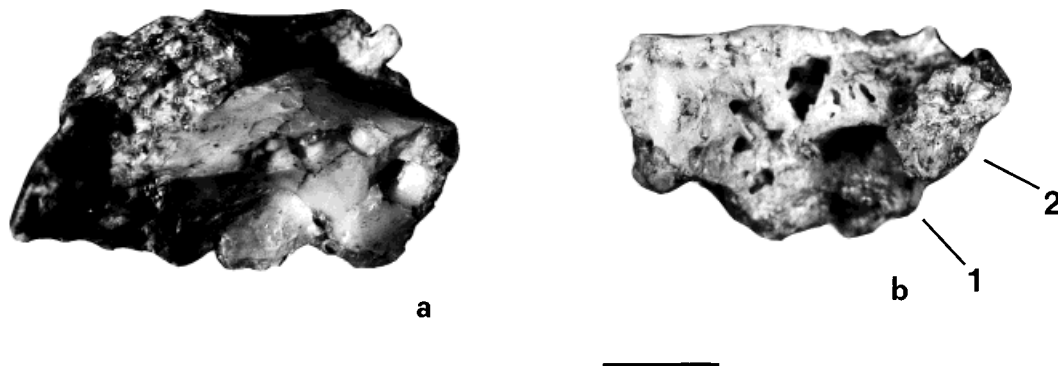


Fig. 7. Petrous part of the left temporal bone, superior (a) and anterior views (b). 1 = external acoustic meatus; 2 = postglenoid process. Scale bar = 1 cm.

meatus and the tip of the postglenoid process (measured along a sagittal plane passing through the most lateral point of the tympanic plate) is 11 mm.

The bone at the level of the base of the mastoid process is thick medio-laterally (about 10 mm) and its thickness decreases gradually superiorly. At the superior edge of the broken surface the thickness is about 3 mm. The lateral edge of the posterior root of the zygomatic emerges at the level of the external acoustic meatus, and it extends anteriorly and laterally for some 15 mm before it is interrupted by a break. The anterior root of the zygomatic projects markedly in a lateral direction for some 9 mm, and then is broken. The zygomatic process is supero-inferiorly convex and thick (about 5 mm at the level of the mandibular fossa). Its superior margin is fairly sharp, and its superior surface is wide and concave medio-laterally.

In basal view the posterior portion of the fragment shows pneumatization of the mastoid process, with some air-cells still filled with matrix. The postglenoid process forms the posterior edge of a broad and shallow mandibular fossa. The dimensions of the mandibular fossa are about 13.3 mm in length (12 mm—no. 80 of Wood, 1991a) and about 17 mm in breadth (16 mm—no. 82 of Wood, 1991a). The articular eminence is very low and almost flat mediolaterally. Medially it slopes markedly down to a weak entoglenoid process. Posterior to the entoglenoid process, a bony edge outlines the mar-

gin of the petrosquamous fissure, running for 8 mm before being broken. Anterior to the entoglenoid process the margin of the petrosquamous fissure continues for about 6 mm to the projecting tip of a temporal spine (equivalent to the sphenoid spine in humans). Anterior to the temporal spine, the fragment is broken along the sphenosquamosal suture, which clearly bisects the *foramen spinosum* just in front of the temporal spine. The sphenosquamosal suture moves superiorly and then curves laterally outlining a flat preglenoid plane, which slopes markedly superiorly in front of the articular eminence. On the internal aspect of the fragment the only relevant anatomical features appear to be the grooves for the middle meningeal artery. From the *foramen spinosum* the common trunk moves superiorly and posteriorly, and after 10 mm it divides into anterior and posterior branches, which can still be observed for some 8 mm (the anterior), and some 9 mm (the posterior).

**Left temporal bone fragment (Fig. 7).** A fragment of the left temporal bone is present, preserving the petrous part, portion of the superior surface of the external acoustic meatus and most of the postglenoid process.

Also, a smaller fragment is present, which cannot be joined to the larger one, preserving the medial part of the inferior wall of the external acoustic meatus and part of the petrous crest.

The petrous part is moderately well preserved. The superior margin is abraded,

more so in the medial part, but laterally it appears to have been acuminate. On the anterior surface a low, rounded arcuate eminence is evident. The posterior surface, vertically oriented, is markedly abraded in its medial portion, where a section of the internal acoustic meatus is evident as a large, rounded opening, 4.4 mm in diameter. Posterior and lateral to it a rather deep and concave *impressio cerebellaris* (Weidenreich, 1943) is present, limited anteriorly by the large, curved aperture of the vestibular aqueduct. On the inferior aspect, part of the smooth superior surface of the external acoustic meatus (extending for some 18 mm mediolaterally) can be observed. The outline of the preserved portion of the meatus is circular. Medial to the internal margin of the external acoustic meatus, the internal structure of the petrous bone is exposed, partially filled with matrix which obscures some anatomical details. Among the features that can be observed are the mastoid antrum, part of the facial canal, part of the *tensor tympani* canal, a relatively small oval window, a large promontory, the round window, the tympanic sinus, and part of the lateral wall of the carotid canal.

The detailed description of the internal structure of the petrous bone will be presented elsewhere, after a careful cleaning of this area has been carried out.

The postglenoid process, similar to the right, is markedly projecting and subtriangular in sagittal section. It is broken on its medial margin, resulting in an irregular outline in anterior view. On this isolated specimen, the orientation of the petrous axis cannot be determined.

On the inferior aspect of the smaller fragment, a distinct petrous crest is evident.

#### MORPHOLOGICAL COMPARISONS

A number of morphological and metrical comparisons have been carried out in order to indicate the systematic position of Stw 151. The comparisons were aimed at evaluating whether the specimen, which is believed to derive from Member 4, could be assigned to the species *A. africanus* or whether it shows a significant number of features allowing its attribution to one of the other taxa which have been considered by

some authors to be present in the Member 4 deposit, namely early *Homo* (Kimbel and Rak, 1993) or an ancestor of the "robust" australopithecines (Clarke, 1988).

For these reasons the teeth and the other skull fragments have been compared with the published specimens of South African early hominids, namely *A. africanus* from Sterkfontein, Makapansgat and Taung; *A. robustus* from Swartkrans and Kromdraai; early *Homo* from Sterkfontein and from Swartkrans. Where necessary, however, comparisons with early *Homo* specimens from East African sites have also been made (especially because of the relatively small number of available teeth of early *Homo* from South Africa). For the metrical analysis of the dentition the entire sample of South African hominids, including undescribed specimens from Sterkfontein has been utilized (Table 3). Metrical data on the dentition of South African hominids have been collected by the first author; data on *H. habilis* are from Tobias (1991); data on *H. rudolfensis* are from Wood (1991a) and Broome et al. (1995).

#### Deciduous teeth

The morphology of the deciduous teeth of Stw 151 closely resembles that of juvenile individuals of *A. africanus*, in particular Sts 24/24a. There are, however, some differences.

In the upper canine a mesial interproximal attrition facet is present, indicating the lack of a  $di^2-d^c$  diastema, a condition different from that of the Taung child and more similar to that of OH 39 and OH 4, two *H. habilis* specimens from Olduvai (Grine, 1984).

The  $dm^1$  is virtually identical to that of Sts 24/24a, apart from the lack of a V-shaped buccal depression surrounding the principal buccal groove (a feature described by Grine, 1984, as typical of *A. africanus*).

The  $dm^2$  is also remarkably similar to that of Sts 24/24a. Many other  $dm^2$ s of early South African hominids are available for metrical comparisons to be made. The diameters of Stw 151 fall towards the lower end of the distribution for *A. africanus*, and well outside the limits of the distribution for *A. robustus*. Only the MD diameter of Taung is

TABLE 3. Comparative dental measurements (MD and BL diameters) of South African early fossil hominids. *Homo* refers to South African specimens of early *Homo*. Data on Stw 151 are not included

|                      |                     | md |          |      |           | bl |          |      |           |
|----------------------|---------------------|----|----------|------|-----------|----|----------|------|-----------|
| Tooth                | Taxon               | n  | <i>x</i> | S.D. | Range     | n  | <i>x</i> | S.D. | Range     |
| Deciduous maxillary  |                     |    |          |      |           |    |          |      |           |
| c                    | <i>A. africanus</i> | 2  | 7.02     | —    | 6.7–7.3   | 2  | 6.14     | —    | 6.0–6.3   |
|                      | <i>Homo</i>         | —  | —        | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | —  | —        | —    | —         | —  | —        | —    | —         |
| dm1                  | <i>A. africanus</i> | 3  | 9.15     | 0.70 | 8.6–9.9   | 3  | 9.77     | 0.41 | 9.3–10.0  |
|                      | <i>Homo</i>         | —  | —        | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 1  | 9.10     | —    | —         | 1  | 10.10    | —    | —         |
| dm2                  | <i>A. africanus</i> | 5  | 10.80    | 0.91 | 9.5–11.6  | 4  | 11.31    | 0.25 | 11.0–11.5 |
|                      | <i>Homo</i>         | 3  | 10.98    | 0.56 | 10.4–11.4 | 3  | 11.15    | 0.15 | 11.0–11.3 |
|                      | <i>A. robustus</i>  | 6  | 10.98    | 0.41 | 10.4–11.4 | 6  | 12.08    | 0.41 | 11.5–12.7 |
| Deciduous mandibular |                     |    |          |      |           |    |          |      |           |
| c                    | <i>A. africanus</i> | 2  | 6.50     | —    | 6.4–6.6   | 2  | 5.55     | —    | 5.4–5.7   |
|                      | <i>Homo</i>         | —  | —        | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 5  | 5.80     | 0.46 | 5.0–6.2   | 5  | 5.10     | 0.44 | 4.6–5.8   |
| dm1                  | <i>A. africanus</i> | 4  | 8.79     | 0.33 | 8.5–9.1   | 4  | 7.66     | 0.33 | 7.3–8.0   |
|                      | <i>Homo</i>         | —  | —        | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 9  | 10.19    | 0.46 | 9.4–11.0  | 9  | 8.37     | 0.62 | 7.9–9.8   |
| dm2                  | <i>A. africanus</i> | 7  | 11.85    | 0.82 | 10.6–12.8 | 7  | 10.14    | 0.63 | 9.0–11.0  |
|                      | <i>Homo</i>         | —  | —        | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 12 | 12.77    | 0.50 | 11.9–13.6 | 12 | 10.54    | 0.71 | 9.7–12.1  |
| Permanent maxillary  |                     |    |          |      |           |    |          |      |           |
| I1                   | <i>A. africanus</i> | 10 | 10.71    | 0.96 | 9.4–12.5  | 9  | 8.60     | 0.42 | 8.0–9.3   |
|                      | <i>Homo</i>         | 2  | 10.53    | —    | 10.3–10.8 | 2  | 7.04     | —    | 6.5–7.6   |
|                      | <i>A. robustus</i>  | 11 | 9.02     | 0.63 | 8.2–9.8   | 10 | 7.36     | 0.51 | 6.3–8.1   |
| I2                   | <i>A. africanus</i> | 10 | 6.82     | 0.69 | 5.8–8.1   | 9  | 6.90     | 0.55 | 5.8–7.7   |
|                      | <i>Homo</i>         | 3  | 6.89     | 1.22 | 5.5–7.8   | 3  | 7.36     | 0.12 | 7.3–7.5   |
|                      | <i>A. robustus</i>  | 8  | 6.65     | 0.64 | 5.9–8.1   | 8  | 6.60     | 0.63 | 5.8–7.9   |
| C                    | <i>A. africanus</i> | 15 | 10.07    | 0.70 | 8.8–11.1  | 14 | 10.60    | 1.24 | 8.9–12.7  |
|                      | <i>Homo</i>         | 1  | 10.72    | —    | —         | 1  | 10.29    | —    | —         |
|                      | <i>A. robustus</i>  | 17 | 8.54     | 0.57 | 7.4–9.7   | 17 | 9.38     | 0.75 | 8.4–11.1  |
| P3                   | <i>A. africanus</i> | 27 | 9.20     | 0.54 | 7.9–10.6  | —  | —        | —    | —         |
|                      | <i>Homo</i>         | 1  | 9.56     | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 16 | 9.97     | 0.45 | 9.3–11.1  | —  | —        | —    | —         |
| M1                   | <i>A. africanus</i> | 22 | 12.95    | 0.70 | 11.4–14.4 | 24 | 13.98    | 0.74 | 12.7–15.1 |
|                      | <i>Homo</i>         | 5  | 13.28    | 0.40 | 12.7–13.7 | 4  | 12.89    | 0.55 | 12.2–13.4 |
|                      | <i>A. robustus</i>  | 19 | 13.25    | 0.47 | 12.4–13.9 | 19 | 14.84    | 0.67 | 13.3–16.8 |
| M2                   | <i>A. africanus</i> | 23 | 14.37    | 1.20 | 12.6–16.9 | 27 | 16.03    | 1.30 | 13.5–18.6 |
|                      | <i>Homo</i>         | 1  | 13.70    | —    | —         | 2  | 14.55    | —    | 14.3–14.8 |
|                      | <i>A. robustus</i>  | 19 | 14.16    | 0.84 | 12.8–15.7 | 19 | 16.05    | 0.77 | 14.5–17.0 |
| Permanent mandibular |                     |    |          |      |           |    |          |      |           |
| I1                   | <i>A. africanus</i> | 9  | 6.29     | 0.40 | 5.6–6.9   | 10 | 6.70     | 0.64 | 5.9–7.9   |
|                      | <i>Homo</i>         | 1  | 5.96     | —    | —         | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 8  | 5.45     | 0.22 | 5.2–5.9   | 8  | 6.30     | 0.43 | 5.5–6.7   |
| I2                   | <i>A. africanus</i> | 11 | 7.44     | 0.32 | 6.9–8.1   | 13 | 8.05     | 0.69 | 6.8–9.2   |
|                      | <i>Homo</i>         | 2  | 6.99     | —    | 6.9–7.1   | —  | —        | —    | —         |
|                      | <i>A. robustus</i>  | 6  | 6.03     | 0.42 | 5.6–6.6   | 6  | 6.97     | 0.40 | 6.5–7.5   |
| C                    | <i>A. africanus</i> | 23 | 9.45     | 0.63 | 8.4–10.7  | 25 | 10.19    | 0.78 | 8.8–12.2  |
|                      | <i>Homo</i>         | 2  | 8.30     | —    | 8.3–8.3   | 1  | 8.98     | —    | —         |
|                      | <i>A. robustus</i>  | 11 | 7.55     | 0.57 | 6.9–8.7   | 11 | 7.88     | 0.66 | 7.2–9.2   |
| P3                   | <i>A. africanus</i> | 19 | 9.71     | 0.70 | 8.6–11.1  | 18 | 11.06    | 1.16 | 9.3–13.5  |
|                      | <i>Homo</i>         | 2  | 9.45     | —    | 8.8–10.1  | 2  | 10.34    | —    | 10.0–10.7 |
|                      | <i>A. robustus</i>  | 16 | 10.12    | 0.53 | 9.0–11.4  | 16 | 11.86    | 0.75 | 10.4–12.8 |
| P4                   | <i>A. africanus</i> | 22 | 10.39    | 0.87 | 8.9–12.1  | 21 | 11.48    | 0.87 | 10.0–13.2 |
|                      | <i>Homo</i>         | 1  | 10.00    | —    | —         | 1  | 9.78     | —    | —         |
|                      | <i>A. robustus</i>  | 14 | 11.31    | 0.59 | 10.7–12.3 | 14 | 12.89    | 0.99 | 11.6–14.7 |
| M1                   | <i>A. africanus</i> | 29 | 14.05    | 0.95 | 12.4–15.5 | 31 | 13.06    | 1.03 | 10.5–15.1 |
|                      | <i>Homo</i>         | 2  | 13.45    | —    | 13.3–13.6 | 2  | 11.90    | —    | 11.9–11.9 |
|                      | <i>A. robustus</i>  | 24 | 14.84    | 0.89 | 12.9–16.7 | 23 | 13.55    | 0.94 | 11.8–15.5 |

slightly smaller than those of Stw 151, but this is probably due to the marked reduction of the hypocone in the Taung  $dm^2$ , which also affects its MD dimensions.

In the lower canine a tiny lingual tubercle is evident, a feature not present in Taung and Sts 24/24a. This feature probably affects the BL diameter, which is larger than in the latter specimens, whereas the MD is smaller than in both of them.

In the  $dm_1$  all of the features distinguishing *A. africanus* from the "robust" australopithecines are evident, among which are the mesial position of the protoconid in respect to the metaconid, the *fovea anterior* skewed lingually, the protuberant *tuberculum molare* (Grine, 1984, 1985). Metrically these teeth closely resemble those of *A. africanus* specimens and are well below the limits of the distribution of *A. robustus*.

The  $dm_2$ s also show overall morphological similarities with the other *A. africanus* specimens, the only difference being the more mesially positioned protoconid relative to the metaconid in Stw 151. The existence of a "double anterior fovea" and of a mesial buccal groove ending abruptly in a shelf suggest also differences from early *Homo* specimens from East Africa (Grine, 1984). The measurements of these teeth match well with other *A. africanus* specimens (Sts 24/24a, Stw 97), and are clearly distinct from those of *A. robustus*.

Thus, the morphological and metrical analysis of the deciduous teeth indicates, overall, close affinities with *A. africanus* specimens, and major differences from *A. robustus*.

#### Permanent teeth

The upper central incisors of Stw 151 compare with the smallest of the *A. africanus* sample ( $n = 9$ ), as indicated by the MD and the BL dimensions. When the two dimensions are plotted (Fig. 8), this is indeed the only specimen of supposed *A. africanus* showing an overlapping of these measurements with the distribution of *A. robustus* ( $n = 10$ ), which is known for having relatively small incisor teeth. At the same time, for the BL dimension Stw 151 is separated from *A. africanus* specimens suggesting some degree of BL reduction compared to *A. africa-*

*nus*, as in two *Homo* specimens from Swartkrans.

The morphology of  $I^2$  shows strong similarities with the corresponding teeth of *A. africanus* specimens, in particular Sts 52 and Sts 24, although the mesial marginal ridge is less developed, and the incisal edge more rounded than in Sts 24. The measurements of the lateral incisors fall also at the lower end of the distribution for *A. africanus*, which largely overlaps that of *A. robustus*.

In the upper canine the lingual face shows what Robinson (1956) considered to be a feature typical of *A. africanus*, that is "a prominent raised, rounded ridge or swelling running from the apex up the lingual face slightly mesialward of the centre" (Robinson, 1956, p. 45). A lingual tubercle, as evident on Stw 151, can also be observed in the canines of Sts 52 and MLD 11/30. The metrical features of the upper canine are again at the lower limit of the distribution of *A. africanus*, overlapping with *A. robustus*.

Although only parts of the upper third premolars can be observed on this specimen, the buccal face shows a narrowing towards its cervix typical of *A. africanus* (Robinson, 1956), but it lacks the well-defined buccal grooves evident in *A. africanus* specimens.

The upper molars show many morphological features commonly found in *A. africanus*, but not in *A. robustus*. These include, in the first molar, a marked Carabelli trait, a mesial crest connecting the protocone and the paracone, and a parastyle. The buccal groove gradually fades, as in Sts 24; it differs from *A. africanus* specimens, such as TM 1512, which have the buccal groove bounded mesially by a more or less marked mesial ridge. The *crista obliqua* is interrupted, as in *A. africanus* specimens with unworn (or slightly worn) M's (Wood and Engleman, 1988). In this respect it is interesting to note that all the South African specimens attributed to *Homo* (SE 255, SK 27, SKX 268, SKW 3114) show an interrupted *crista obliqua*, whereas an uninterrupted *crista obliqua* has been reported in seven of eight specimens of *Homo* from East Africa (Wood and Engleman, 1988). The MD and BL diameters of the first molars of Stw 151 have similar values. A bivariate plot of the MD and BL



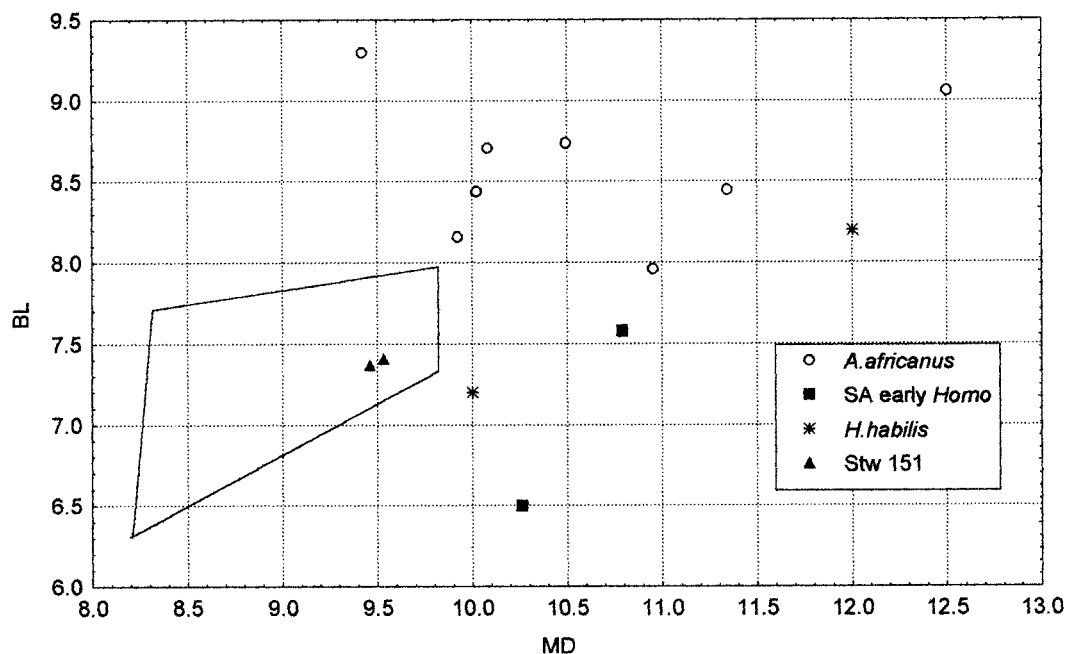


Fig. 8. Bivariate plot of MD and BL diameters of upper central incisors in some fossil Hominid species. Area enclosed among solid lines indicates the distribution for *A. robustus*.

diameters of the first molars of South African hominids and *Homo habilis* from Olduvai and Koobi Fora (Fig. 9) separates Stw 151 from *A. robustus* specimens, sets it at the margin of the *A. africanus* sample and inside the distribution for early *Homo*. These results suggest a relative reduction in the BL direction and MD elongation, the latter considered to be a feature typical of *H. habilis* (Tobias, 1991).

In the second molar, an evidently asymmetric, rhomboidal crown outline is present. This feature is considered to be typical of early *Homo* by Kimbel et al. (1997). The metacone is reduced and subdivided into two small cuspules (as in Sts 52); a protoconal cingulum is present, although less developed than in *A. africanus* specimens. The dimensions of the second molar, too, fall towards the lower end of the distribution for *A. africanus*, very close to the values of Se 1508, an early *Homo* specimen from Sterkfontein Member 5. The range of variability of the second molars is higher than in the first, so that the distributions of *A. robustus* and *A. africanus* largely overlap.

In the lower teeth, the central incisors reveal notable morphological affinities with Sts 24, including the faint ridge in the centre of the lingual face and the five mamelons on the incisal edge. Minor differences are the lingual concavity (less marked than in Sts 24) and the crown height, which is higher in Sts 24 (11.6 mm) than in Stw 151 (right 10.4, left 10.8 mm). As for the tooth diameters, the MD is among the smallest, and the BL the smallest of the entire Sterkfontein sample. The resulting Crown Shape Index ( $LI_1 = 103.7$ ;  $RI_1 = 105.1$ ) falls outside the *A. robustus* range (77.6–98.2;  $n = 8$ ).

The lateral incisors, too, are smaller than all *A. africanus* homologues in both MD and BL diameters, with a Crown Shape Index value (102.3) that clearly differentiates them from *A. robustus* (80–90.3;  $n = 6$ ). A rounded distal end of the incisal edge, a distinguishing trait for *A. africanus*, is present on both of them.

The lower canines share numerous morphological traits with *A. africanus* specimens (Sts 50, Sts 51), such as a distinct cusplet on the distal edge of the crown and a

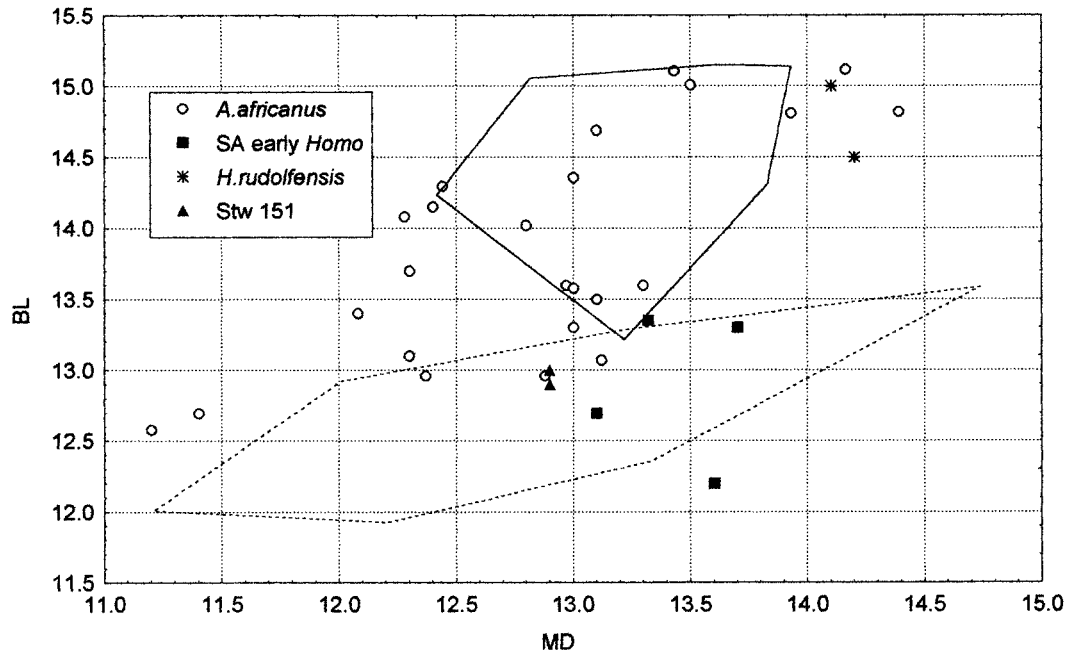


Fig. 9. Bivariate plot of MD and BL diameters of upper first molars in some fossil Hominid species. Area enclosed among solid lines indicates the distribution for *A. robustus*. Area enclosed among dashed lines indicates the distribution for *H. habilis*.

well-developed lingual ridge, but differ in being less asymmetrical and more pointed. The metrical features, on the other hand, being among the smallest of the whole Sterkfontein sample, overlap with the upper end of the distribution for *A. robustus*.

The third premolar shows an asymmetrical crown, a well-defined lingual cusp placed mesially to the buccal cusp, and buccal grooves, as in other *A. africanus* third premolars. These features are described by Suwa et al. (1996) as common to both *A. africanus* and early *Homo*; Stw 151 lacks, however, the features of early *Homo* considered to be uniquely derived (Suwa et al., 1996). An obvious difference is the presence of a deep median longitudinal fissure, which has been described as a peculiarity of "robust" australopithecines (Wood and Uytterschaut, 1987). Similarly, the existence of additional cusplids on the distal marginal ridge has been reported as a feature more commonly found in the lower premolars of "robust" australopithecines (Wood and Uytterschaut, 1987). With regard to metrical features, a bivariate plot of the MD and BL diameters of the P<sub>3</sub> of

*A. africanus*, *A. robustus*, *Homo* from SK and *H. habilis* from Olduvai (Fig. 10) shows a number of interesting points: 1) Stw 151 falls well outside the range of distribution for *A. robustus*; 2) it is again among the smallest specimens of *A. africanus*; and 3) it (and a few other specimens, such as Sts 24) falls very close to the distribution for *H. habilis*, suggesting some degree of BL reduction.

Similar morphological observations apply also to the P<sub>4</sub>, with a number of features comparable to *A. africanus*, including buccal grooves equally well developed. A morphological affinity with the *H. habilis* specimen OH 7 is evident in the distal marginal ridge with four distinct cusplids present. Five additional cusplids are also present on the distal marginal ridge of the RP<sub>4</sub> of a *Homo* specimen from Swartkrans (SKX 21204).

The MD and BL diameters (still among the smallest of *A. africanus*) clearly distinguish this specimens from *A. robustus*. A bivariate plot (Fig. 11) also sets Stw 151 at the margins of the *A. africanus* sample.

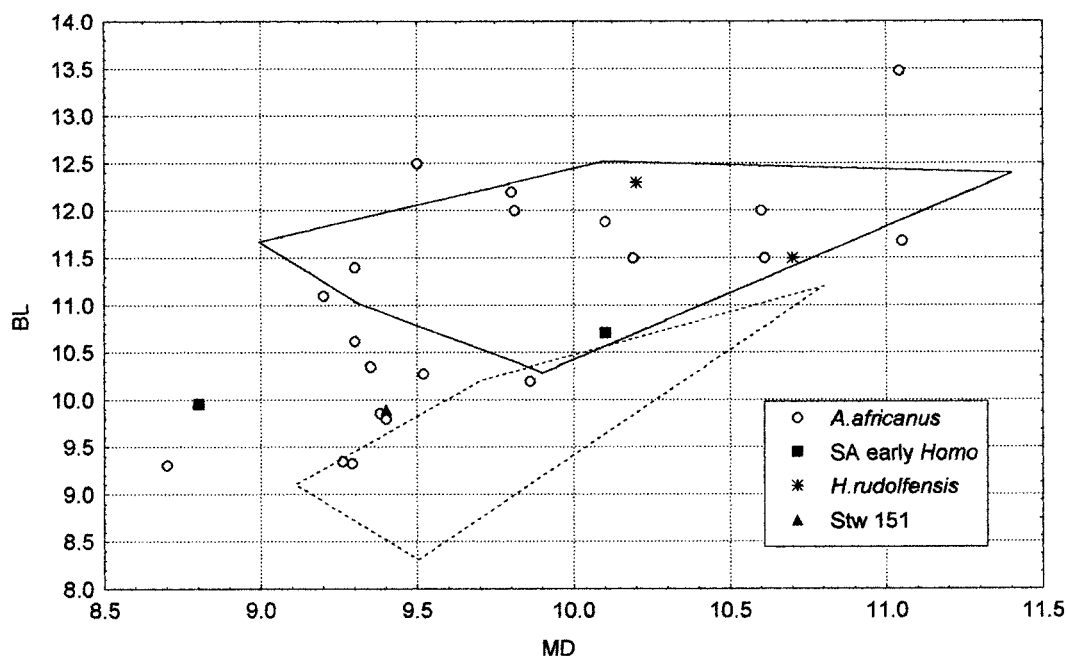


Fig. 10. Bivariate plot of MD and BL diameters of lower third premolars in some fossil Hominid species. Area enclosed within solid lines indicates the distribution for *A. robustus*. Area enclosed within dashed lines indicates the distribution for *H. habilis*.

The development of the talonid of the lower premolars in early hominids has been estimated in different ways by many authors, some using linear (e.g., Robinson, 1956; Sperber, 1973; Tobias, 1991) and others area measurements (e.g., Wood and Uytterschaut, 1987; Suwa, 1988). Using area measurements, Wood and Uytterschaut (1987) have shown that the relative development of the talonid is weak in early *Homo*, intermediate in *A. africanus* and quite marked in "robust" australopithecines, with corresponding degrees of molarisation of the premolars in the three groups. Similar conclusions were reached by Tobias (1991) using the talonid/crown length index (T/CLI), a different way of estimating relative development of the talonid through linear measurements. The T/CLI for the  $P_3$  of Stw 151 (35.1) falls just outside the range for *H. habilis* (26–34.3;  $n = 4$ ), (calculated on the basis of the data presented by Tobias, 1991) and also outside the range for *A. africanus* (26.4–33.3;  $n = 8$ , as calculated by the authors). Similarly, the T/CLI for the  $P_4$  (37.5) falls in the upper part of the range reported

by Tobias (1991) for *A. africanus* (30.6–37.9;  $n = 3$ ), and outside the range for *H. habilis* (30.6–35.9;  $n = 6$ ).

Thus, the lower premolars of Stw 151 seem to show some degree of reduction of the BL diameter compared to the majority of the *A. africanus* sample, but at the same time a marked relative development of the talonid.

The morphological features of the lower first molars show some affinities with *A. africanus* specimens, but also some differences. The affinities include a well-defined posterior fovea, a modified Y fissure pattern and an almost vertical buccal face; differences are evident in the lack of a well-developed trigonid crest and of a protostylid (or any protoconid cingulum) and in the presence of a *tuberculum intermedium*, which, among *A. africanus*, is present only in the Taung child. The most striking differences, however, are in the dimensions of the teeth. A bivariate plot of MD vs. BL diameters (Fig. 12) clearly shows the distinct position of Stw 151 as compared to *A. africanus* specimens, indicating the existence of marked MD elongation, more marked than

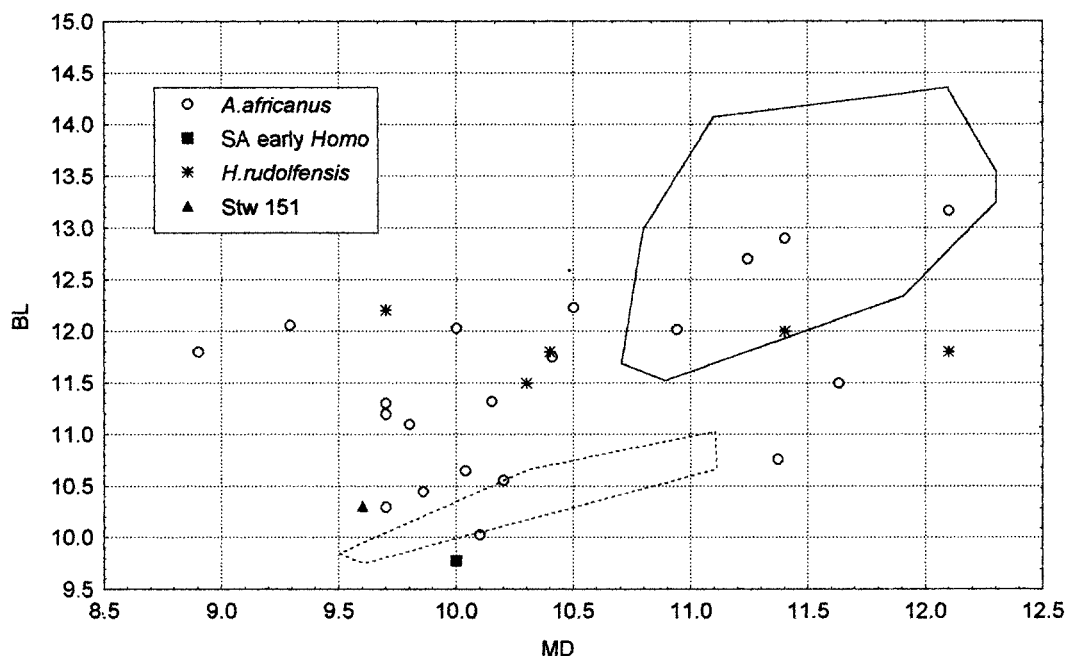


Fig. 11. Bivariate plot of MD and BL diameters of lower fourth premolars in some fossil Hominid species. Area enclosed within solid lines indicates the distribution for *A. robustus*. Area enclosed within dashed lines indicates the distribution for *H. habilis*.

*Homo* specimens from Swartkrans (SK 15, SKX 257 and SKX 258), and within the range of *Homo* specimens from Olduvai. It also falls outside the range of distribution for *A. robustus*. The BL reduction and the MD elongation of  $M_1$ , point to differences from both *A. africanus* and *A. robustus* and similarities with early *Homo* (Tobias, 1991; Wood, 1992, 1993). Some authors (White et al., 1981; Suwa et al., 1996) consider buccolingual narrowness of  $M_1$  a stronger argument of affinities with early *Homo* than the BL reduction of lower premolars.

#### The other cranial fragments

Morphological comparisons of the other skull fragments of Stw 151 (ascending ramus of the mandible, glenoid fossa and petrous bone) with other fossil hominids should theoretically be carried out by the analysing of juvenile specimens of a similar ontogenetic age, since it is known that in primates the areas under consideration are subject to bone remodelling during growth (Weidenreich, 1943; Enlow, 1982; Bromage, 1985).

For example, ontogenetic changes in the morphology of the glenoid fossa have been described and discussed for hominoids by Weidenreich (1943). He noted that "infantile anthropoids [hominoids] have a real fossa which vanishes as their age increases" (Weidenreich, 1943, p. 201). Among early hominids a similar condition can be observed if one compares, for example, the mandibular fossa of the juvenile specimen AL 333-105 of *A. afarensis* with an adult specimen such as AL 333-45. Similarly, a marked petrous crest is evident on the temporal bone of young chimpanzees, whereas its expression is markedly reduced in specimens of older age (at least in the admittedly small sample available for comparison).

These examples indicate that, in some areas of the skull, it is not possible to infer the adult morphology from the juvenile condition.

The restriction of comparison to juveniles reduces the number of potential comparisons, since we have very few juvenile specimens of fossil hominids where the areas under consideration are preserved. Observa-

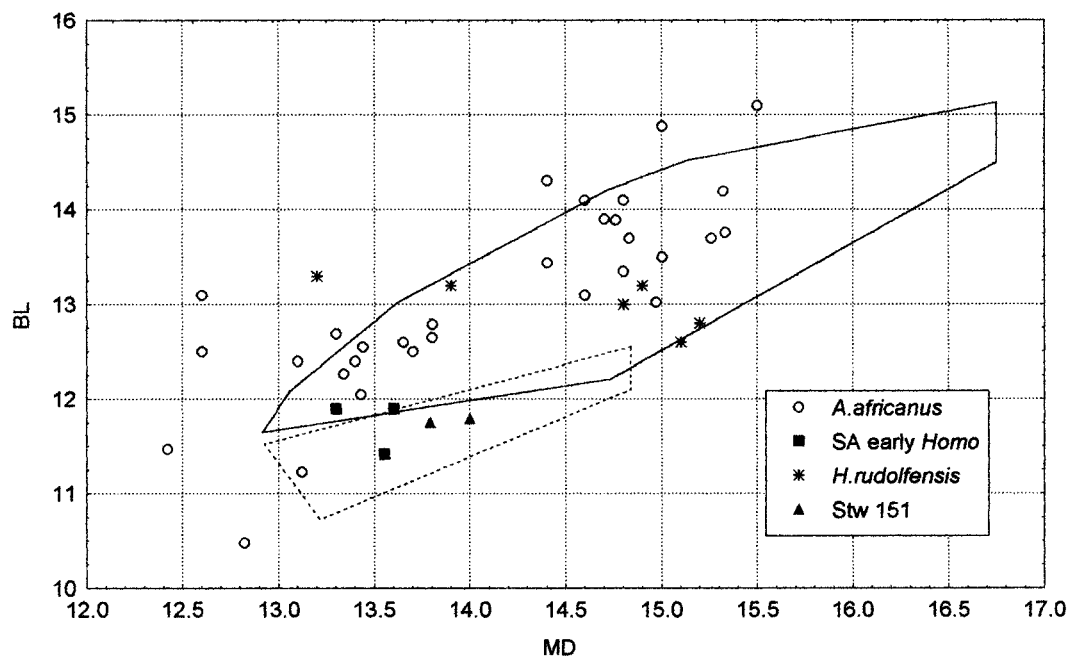


Fig. 12. Bivariate plot of MD and BL diameters of lower first molars in some fossil Hominid species. Area enclosed within solid lines indicates the distribution for *A. robustus*. Area enclosed within dashed lines indicates the distribution for *H. habilis*.

tions of these anatomical areas have thus been carried out on both juvenile and adult specimens of early fossil hominids. Where differences can be observed, however, it is generally difficult to determine whether these can be considered as systematically relevant or only due to the different ages of the specimens.

Stw 151 is one of the few juvenile specimens of early fossil hominids where a fairly complete ascending ramus of the mandible is preserved.

Its lateral surface shows similarities with the mandible of the Taung child in the morphology of the condyle, but the mandibular notch is antero-posteriorly wider in Stw 151 and the coronoid process is less everted. The juvenile *A. robustus* SK 63 has a relatively well-preserved ramus, showing a shallower mandibular notch and an antero-posteriorly broader coronoid process than in Stw 151.

On the medial surface of the ramus of Stw 151, a bony lip is present anterior to the mandibular foramen. This feature is clearly more marked on the exposed portion of the

medial surface of the mandibular ramus of the Taung child, where it may even be described as an incipient lingula. A bony plate, rather than a lingula, is present in this position in adult specimens of *A. africanus* (Sts 52, Sts 36) and in the *H. habilis* specimen OH 13 (Tobias, 1991). Interestingly, an incipient lingula is evident also on the mandibular fragment of Stw 53 (assigned to *H. cf. habilis*). Three features, the *torus triangularis rami*, the *crista endocoronoidea* and the *tuberculum pterygoideum inferius*, are relatively more marked in Stw 151 than in the young adult Sts 52. The medial face of SK 63 differs from Stw 151 mainly in that the *crista endocoronoidea* terminates below the coronoid process (as in SK23, an adult *A. robustus* specimen), whereas in Stw 151 (and also in Sts 52, and in Stw 53) it ends on the coronoid. The anterior edge of SK 63 is more everted, with marked muscular insertions on its lateral portion.

In posterior view, the condyle of Stw 151 is higher and the condylar neck slightly thicker than in the younger Taung child. Its axis



shows the same infero-medial orientation as in the Taung child, whereas in adult specimens of *A. africanus*, such as Sts 52, the axis is almost horizontal. Differences from the published description and photographs of the Hadar hominid AL 333-43b are evident in the narrower and deeper mandibular notch, in the height difference between the higher apex of the coronoid and the condyle, and in the much broader coronoid process than in Stw 151 (White and Johanson, 1982).

The glenoid region of Stw 151 can be compared with that of the juvenile specimen of *A. afarensis* AL 333-105 and also with that of the Taung child.

Part of the medial wall of the right mandibular fossa can be observed on the inferior surface of the natural endocast of the Taung child. The entoglenoid process is evident and, a few millimeters anteromedially, the position of the *foramen spinosum*. This condition differs from that of Stw 151, where the *foramen spinosum* is situated some 15 mm anteriorly and inferiorly to the entoglenoid process; also, in Stw 151 between the two a temporal spine is evident. In this respect, the condition seen in the Taung child is more similar to that present in the juvenile specimen AL 333-105, since in neither case can a marked temporal spine be observed.

The different development of the entoglenoid process relative to the temporal spine has been accurately described in adult specimens of fossil hominids by Tobias (1991). A definite sphenoid spine, inferomedial to the entoglenoid process, is present in *H. habilis* (OH 24 and OH 13), whereas in both *A. africanus* and *A. robustus* it has been described as a small protuberance "satellite" to the entoglenoid process (Tobias, 1991). The condition of Stw 151 suggests stronger similarities with *Homo*, whereas that of Taung (and also of AL 333-105) recalls those of both *A. africanus* and *A. robustus*.

In Stw 151 and in AL 333-105 the *foramen spinosum* is split by the sphenosquamosal suture. This condition is equivalent to that described by Tobias (1991) for *H. habilis* and *A. robustus*, in which the *foramen spinosum* is bounded mainly by the temporal squama, partly by the alisphenoid; whereas in *A.*

*africanus* it is bounded entirely by the squama.

The development of the postglenoid process of Stw 151 is more marked than in the AL 333-105 juvenile, and it is as developed as in some adult specimens of *A. africanus* (MLD 37/38, Sts 71). This feature is variable among early hominids (Tobias, 1991).

Stw 151 has a mandibular fossa slightly deeper than that of AL 333-105. Both *H. habilis* and *A. africanus* are described as having shallow mandibular fossae, contrary to the deep fossa of *A. robustus* (Tobias, 1991).

The articular eminence is more prominent in Stw 151 than in AL 333-105 and also, the preglenoid plane is notably steep, resulting in an acute angle between the preglenoid plane and the anterior wall of the mandibular fossa. This angle is described as acute in *H. habilis* and obtuse in both *A. africanus* and *A. robustus* (Tobias, 1991).

The position of the mandibular fossa relative to the side wall of the brain-case can be compared in Stw 151, in the Taung child and also in AL 333-105. In Stw 151 almost half of the mandibular fossa lies outside the side wall of the brain-case, whereas in both the Taung child and AL 333-105 the mandibular fossa lies almost entirely inside the lateral wall. In adult specimens, the condition as observed in Stw 151 is more similar to *A. robustus*, whereas the Taung child recalls the condition as described for *H. habilis*, with *A. africanus* showing a situation intermediate between the two (Tobias, 1991).

Contrary to AL 333-105, Stw 151 lacks a suprameatal crest. In this region, the posterior root of the zygomatic emerges more anteriorly in AL 333-105 than in Stw 151. This feature in *H. habilis* tends to be more anteriorly placed than in *A. africanus* and in *A. robustus* (Tobias, 1991).

The base of the zygomatic process is thicker in Stw 151 than in AL 333-105. Its lateral extension can be compared with that of the Taung child, the latter being far less projecting laterally from the cranial wall (approx. 4 mm) than in Stw 151. The lateral bulge of the zygomatic is reported by Tobias (1991) to be slender in *H. habilis*, strong in *A. africanus*, and very strong in *A. robustus*,

being related to the development of the masticatory muscles.

On the internal aspect of the fragment, differences between AL 333-105 and Stw 151 are evident in the length of the common meningeal trunk, which is reported to be 4 mm long in AL 333-105 (Kimbél et al., 1982), whereas its length in Stw 151 is about 10 mm. The same component is some 9 mm long in the young adult *H. habilis* OH 24 (Tobias, 1991).

The superior margin of the petrous bone of Stw 151 appears to have been acuminate, at least in its lateral portion. In the juvenile *A. afarensis* specimen AL 333-105, the right superior petrosal margin is described as thin and sharp, whereas the left as blunt and rounded (Kimbél et al., 1982). The form of the superior margin of the petrous is variable among early hominid taxa (Tobias, 1991, 1993).

The posterior surface of the petrous in Stw 151 is vertical, as it is in AL 333-105 (as observed on a cast), and it is difficult to determine any difference between them.

The vertical orientation of the posterior petrosal surface of Stw 151 has been quantitatively assessed by Spoor (1993) relatively to the position of the lateral semicircular canal. The value of the angle between the lateral semicircular canal and the posterior petrosal surface for this specimen is 75 degrees (Spoor, 1993). He also pointed out that some changes in the orientation of the surface might have occurred in later phases of the child's development, but, he believed, only in the direction of an even more vertically oriented surface (Spoor, 1993).

On this ground, comparison can be made with adult specimens of South African fossil hominids. Major differences in the vertical orientation of the posterior petrosal surface have been reported by Spoor (1993) between Stw 151 and other specimens from Sterkfontein (including Stw 53 and Sts 19) and *A. robustus* specimens. Closest affinities are described with the specimens SK 847, the partial skull attributed to *Homo* sp. (Clarke, 1977) from Swartkrans and also with modern human values (Spoor, 1993). Clarke (1977), through a purely morphological approach, already pointed out the vertical orientation of the posterior surface of the pe-

trous bone of SK 847, and suggested that it is a feature that distinguishes *A. africanus* from early *Homo*.

On the posterior surface of the petrous, an *impressio cerebellaris* is evident on the cast of AL 333-105 and is more marked than that present in Stw 151. The petrous crest in Stw 151 is distinct, whereas that of AL 333-105 is described as "undifferentiated" (Kimbél et al., 1982). In adult specimens, the petrous crest tend to be more developed in early *Homo* (SK 847, Stw 53, OH 24) and *A. robustus* (SK 46, SK 48, SK83) than in *A. africanus* (MLD 37/38, Sts 5).

#### STATE OF DENTAL ERUPTION, ATTRITION AND ROOT RESORPTION

Stw 151 is at the start of the mixed dentition stage, with erupted deciduous canine, dm1 and dm2 and erupted permanent M1 and I1. The maxillary and mandibular deciduous canines, first and second molars have been in functional occlusion, as evidenced by marked occlusal and interproximal wear. Dentine exposure is evident on all deciduous teeth, and is classified after Hinton (1981) stages as canines 4/5; dm1 5; dm2 3. Differential occlusal wear is present on the deciduous molars, with marked wear on dm1 but modest wear on dm2.

The I1 teeth show small mesial interproximal wear facets with dimensions in mm (breadth, height) I<sup>1</sup> 1.1, 2.1; I<sub>1</sub> 1.3, 2.8. The M1 teeth show both occlusal and mesial interproximal wear facets (Fig. 13). Distinct powerstroke closing (phase I) and opening (phase II) occlusal facets (Kay and Hiiemae, 1974) are present on all cusps, although there is no evidence of dentine exposure. The stage of occlusal wear corresponds to stage 2 (Hinton, 1981). All of the M1 teeth show interproximal wear facets with the following dimensions in mm (breadth; height): RM<sup>1</sup> 4.5; 3.1; LM<sup>1</sup> 4.2; 2.8; LM<sub>1</sub> 4.8; 2.8; RM<sub>1</sub> 4.8 (height not measured due to presence of dm<sub>2</sub>). There was an estimated loss of approximately 0.5 mm of enamel from the mesial approximal surfaces measured in the mesiodistal direction on RM<sup>1</sup> and RM<sub>1</sub>.

In the anterior jaw segments only the permanent central incisors had erupted. These teeth had attained functional occlusion as evidenced by polishing on the labial



Fig. 13. Scanning electron micrograph of  $M_1$  showing occlusal and interproximal wear facets. The mesial interproximal wear facet is 4.8 mm wide, 2.8 mm high and 0.5 mm deep.

surface of the  $LI_1$ , resulting in some loss of perikymata detail on the incisal 2 mm. There is also evidence of vertical scratches up to 3 mm in length extending downwards on the labial face, which may represent *in vivo* tooth wear. The  $I_2$  teeth had started to erupt, penetrating the overlying bone, but they had probably not yet emerged through the gingiva.

#### STAGES OF DENTAL DEVELOPMENT

To facilitate comparisons between this study and others, stages of root development will be given after Moorrees et al. (1963), although it is recognised that such descriptions can only be broad estimates, since the length of the mature root cannot be known.

The  $I^1$  and  $I_1$  had erupted into functional occlusion, and the lateral incisors were unerupted. All incisors have incomplete roots. The roots of  $LI^1$  and  $RI^1$  are 8.9 and 9.8 mm long, and are scored between  $R \frac{1}{2}$  and  $\frac{3}{4}$  complete. The  $LI_1$  and  $RI_1$  are 8.0 and 8.8 mm long, and are scored  $R \frac{3}{4}$ . The  $RI^2$  root is

6.0 mm long and is scored  $R \frac{1}{2}$ . The  $RI_2$  root is 5.5 mm long, and is scored  $R \frac{1}{3}$ .

The maxillary and mandibular canines are complete on their mesial and distal surfaces, but incomplete at the labial enamel cervix, which forms last. The lower right canine ( $R_C$ ) is fractured obliquely at the cervix, with an incomplete crown height of 11.8 mm. The remaining enamel at the distobuccal cervix shows a mosaic of fine cracks, resembling gaps between flagstones, termed "pavement" cracking. This is believed to characterize enamel which has not yet undergone full maturation. Enamel matrix is initially lowly mineralized around 15% by volume, and is highly hydrated around 40%. The most immature enamel is lost post mortem, with the partially mature enamel undergoing considerable shrinkage, causing the cracked pavement appearance. The cervical line is present on the distal surface of  $R_C$  and 1.3 mm of distal root is present. The  $L_C$  is incomplete (crown height 12.0 mm), with pavement cracking at the

labial cervix. The  $L^C$  is incomplete labially (crown height 13.9 mm), and is complete palatally. On the mesial and distal approximal faces 1.8 mm of root are present. The remaining labial enamel is immature, showing pavement cracking.

The  $P^3$  and  $P_3$  have complete crowns with root initiation. The  $LP^3$  has 2.9 mm of distal root formed. The  $P^4$  and  $P_4$  are crown complete. The  $RP_4$  has 1.4 mm of distal root formed, and the  $LP_4$  1.6 mm of mesial root. The  $M^1$  and  $M_1$  were erupted and in functional occlusion, with  $RM_1$  distal root length 11.9 mm;  $LM_1$  11.6 mm;  $RM^1$  mesiobuccal root 11.2 mm, distobuccal root 10.3 mm, palatal root 11.2 mm;  $LM^1$  distobuccal root 10.9 mm, palatal root 10.8 mm, and are root complete, although the root apices are not fully closed. The  $M^2$  crown is complete, with signs of root initiation; with  $RM^2$  showing up to 0.9 mm of developing buccal root, but no palatal root development, and there is evidence of immature enamel at the palatal cervix. The  $LM_2$  distal fragment is crown complete, and there is more than 0.5 mm of lingual root formed, although buccal cervical enamel is still immature. The  $M_3$  germs are not preserved, but careful cleaning of the right mandibular ramus revealed the presumptive crypts of the  $M_2$  and  $M_3$ . The right ramus is fractured vertically in a near coronal plane at the junction with the mandibular body (Fig. 6c). The two crypts are located one above the other, and are open anteriorly. The lower  $M_2$  crypt is 12 mm broad and 10 mm high and lies at the base of the ascending ramus, above the inferior dental canal. The  $M_3$  crypt is small, 7 mm wide mediolaterally, 8 mm high supero-inferiorly and 5 mm deep, and lies inferomedial to the torus triangularis rami. The  $M_2$  crypt is large enough to accommodate the developing  $M_2$ . The  $M_3$  crypt however appears too small to accommodate even a partially formed crown, and was presumably occupied by a tooth germ with no or minimal cuspal mineralization.

#### ESTIMATION OF AGE AT DEATH

Teeth contain internal growth markings of short period, represented by cross-striations which represent daily increments, and longer period striae of Retzius. A number of

studies in hominoids have shown a range of values for daily increments between adjacent striae of between 6 and 12 (Dean et al., 1993; Fitzgerald, 1996), with the majority of studies between 7 and 9, with a modal value of 8 (Beynon, 1992). Perikymata are surface manifestations of striae in imbricational enamel, although they may be inconsistently expressed (Beynon, 1992). Perikymata have been used to estimate crown formation times and age at death in fossil hominids (Bromage and Dean, 1985; Beynon and Dean, 1988; Dean, 1987).

In Stw 151 perikymata are well expressed on the labial surfaces of  $RI_1$ ,  $LI_1$ , and  $R_C$  (although the cervix was fractured) and  $RI^2$  and  $RI_2$ , and variably on  $LI^1$  requiring some interpolation. Perikymata are relatively widely spaced occlusally, averaging 3 to 4 per mm, but become progressively more closely packed cervically, ranging from 12 to 15 per mm at the cervix (Table 4).

No data are available on appositional enamel thickness or appositional enamel formation time in incisors or canines in Stw 151. Appositional enamel formation time in modern human incisors is around 0.5 years (Beynon and Dean, 1991). Appositional enamel formation time in a "robust" australopithecine canine (Dean et al., 1993) is estimated at 305 days (0.84 years). Incisor and canine enamel thickness appears to be greater in australopithecines than in humans (Beynon, personal observation; Dean et al., 1993), and an intermediate estimate for appositional enamel formation time of 0.65 years was used for  $I_1$  and  $I_2$ , and 0.8 years for  $R_C$  in this specimen.

The canine teeth are near crown complete at death, which makes them key teeth in the reconstruction of age at death (Dean et al., 1993). The  $R_C$  show 124 perikymata to the incomplete cervix, and it is estimated that 1 mm of cervical enamel was lost, equivalent to 16 perikymata, making a total of 140 perikymata. This is equivalent to an imbricational enamel formation time of 2.68, 3.07, 3.45 or 3.83 years, using 7, 8, 9, or 10 day periodicities. These values summed with the  $R_C$  appositional enamel formation time of 0.8 years give overall crown formation times of 3.5, 3.9, 4.3 or 4.6 years.



TABLE 4. *Perikymata counts on incisor and canine teeth of Stw 151*

|          | RI <sub>1</sub> | LI <sub>1</sub> | RI <sub>2</sub> | LI <sup>1</sup> | RI <sup>2</sup> | R <sub>C</sub> | L <sub>C</sub> |
|----------|-----------------|-----------------|-----------------|-----------------|-----------------|----------------|----------------|
| Occlusal | (4*)            | (4*)            | (2)             | (3)             | 5               | (3)            | 7              |
|          | 6               | 4               | 6               | (5)             | 7               | (4)            | 7              |
|          | 9               | 6               | 7               | 6               | 7               | 7              | 7              |
|          | 7               | 7               | 7               | (6)             | 8               | 9              | (8)            |
|          | 8               | 7               | 7               | (5)             | 11              | 8              | 10             |
|          | 9               | 9               | 7               | (5)             | 14              | 11             | 11             |
|          | 11              | 11              | 10              | 8               | 16              | 12             | 14             |
|          | 12              | 12              | 11              | 10              | 13              | 15             | 15             |
|          | 11              | 14              | 12              | 12              | 11              |                | 16             |
|          | 13              | 15              | 13              | 12              |                 | 1              | (13)           |
|          | (13*)           | (13)            | 15              | 13              |                 | 15             | (13)           |
|          |                 |                 | 11              | 12              |                 | 14             |                |
|          |                 |                 |                 |                 |                 | 14             |                |
|          |                 |                 |                 |                 |                 | 15             |                |
| Cervical |                 |                 |                 | (14)            |                 |                |                |
| Total    | 103 ± 3         | 102 ± 5         | 108 ± 2         | 111 ± 10        | 92 ± 2          | 124 ± 2        | 121 ± 5        |

Values in parenthesis derive from slightly worn (or damaged) areas where some degree of interpolation has been applied.

The age at death is equal to the crown formation time summed with the period of time between birth and initial mineralization. A range of periods of delay in mineralization in canine teeth in great apes has been reported, reviewed in Dean et al. (1993), from 0.33 to 0.83 years in gorilla and orangutan, and 0.25 to 0.42 years in chimpanzee. In humans there are delays of 0.25 and 0.5 years (Logan and Kronfeld, 1933); Gustafson and Koch (1974) reported a range from 0.33 to 0.55, mean 0.42 years. In this study we initially used an estimate of 0.5 years delay in onset of mineralization in the canine to reconstruct developmental relationships between the lower C and the M<sub>1</sub>, M<sub>2</sub> and I<sub>1</sub> teeth.

The M<sub>1</sub> begins to mineralize shortly before birth in all extant hominoids (Winkler, 1995, and references therein). Crown formation times in M<sub>1</sub> and M<sub>2</sub> were estimated by use of data on cuspal (appositional) enamel in M<sub>2</sub>, and imbricational enamel in M<sub>1</sub> from surface perikymata. The RM<sub>2</sub> crown is fractured obliquely through the metaconid and hypoconulid, and the fracture surface was lightly etched using 0.1 M H<sub>3</sub>PO<sub>4</sub> for 30 seconds, and other tooth surfaces were protected with nail varnish (Beynon, 1987). A Spurr resin replica was prepared (Beynon, 1987) and studied in the SEM. There are 585 ± 10 cross-striations in appositional enamel in the buccal cusp, estimated to take 1.6 years to form. In the RM<sub>1</sub> there are 62 ± 5 perikymata on the distobuccal face, giving an imbricational enamel formation time of 1.2, 1.35, 1.5 or 1.65 years, depending on our

use of 7, 8, 9 or 10 day periodicities respectively. These values combined to give crown formation times of 2.7, 2.96, 3.13 or 3.3 years for the M<sub>1</sub> and M<sub>2</sub>. These lower values at 7 and 8 days are consistent with other histological studies on extant (Beynon et al., 1991; Reid et al., in press) and extinct (Beynon and Dean, 1988; Dean, 1987) hominoids.

To reconstruct relationships between developing teeth in Stw151, the values for age at death derived from the canine tooth, using a 0.5 year delay in mineralization, were plotted on a provisional bar chart (Fig. 14), giving alternative ages at death for this specimen of 4.0, 4.4, 4.8, or 5.1 years with periodicities of 7, 8, 9, or 10 days in imbricational enamel. The M<sub>1</sub> values were introduced, from an assumption of initial mineralization at 0.1 years before birth, and by use of crown formation times of 2.79, 2.96, 3.13 or 3.3 years. The M<sub>2</sub> crown was added, assuming the same crown formation times as used in M<sub>1</sub>. The M<sub>2</sub> crown is complete, with the beginnings of root formation, so 0.1 years was added to these times. These overall times for the M<sub>2</sub> were projected backwards from the estimated age at death, allowing the placement of M<sub>2</sub> relative to M<sub>1</sub>. Using the 0.5 year delay information of the R<sub>C</sub> would result in the M<sub>2</sub> crown beginning to mineralize at 1.1, 1.35, 1.55 or 1.65 years. This would have resulted in considerable overlap in development between the M<sub>1</sub> and M<sub>2</sub>, which is little affected by stria periodicity, ranging from 57, 52, 48 or 47% of the overall crown formation times.



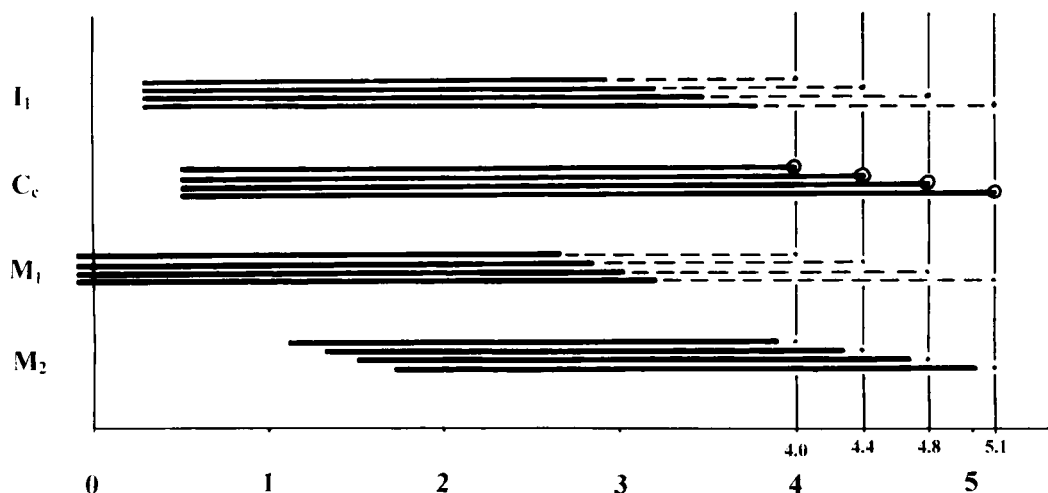


Fig. 14. Preliminary bar chart registered using a 0.5 year interval between birth and first mineralisation of the lower canine. Crown formation times were calculated using 7, 8, 9 and 10 day periodicities between striae, giving provisional ages at death of 4.0, 4.4, 4.8 or 5.1 years.

In modern great apes there is appreciable overlap between all of the molar teeth (Anemone et al., 1996), with the M<sub>3</sub> overlapping the M<sub>2</sub> by up to 50% (Kuykendall, 1996). In contrast, in modern humans the M<sub>1</sub> and M<sub>2</sub> are reported not to overlap in radiographic studies, although histological studies are now showing slight overlap of around 10% (Reid et al., in press); and in European children there is a radiographic gap of 1 or 2 years between completion of M<sub>2</sub> and onset of mineralization in M<sub>3</sub> (Moorrees et al., 1963). However radiographic studies (Fanning and Moorrees, 1969) in Australian Aboriginal children show that the M<sub>3</sub> begins to mineralize 4.3 years earlier, and a histological study on an African showed little separation between M<sub>2</sub> completion and M<sub>3</sub> initiation (Dean et al., 1993). In summary, in the molar tooth series, apes show consistent overlap between molars, whereas humans show minimal overlap between M<sub>1</sub> and M<sub>2</sub>, and variable spacing between M<sub>2</sub> and M<sub>3</sub>.

The preliminary reconstruction in Stw 151, showing marked overlap between the M<sub>1</sub> and M<sub>2</sub>, appears to be inconsistent with the apparent delay in mineralization of the M<sub>3</sub>. A further inconsistency in development when we used the 0.5 year R<sub>C</sub> delay relates to the time available for incisor root development. The I<sub>1</sub> begins to mineralize postna-

tally around 0.3 years in orangutan (Beynon et al., 1991; Winkler, 1995) and chimpanzee (Winkler, 1995); 0.8 years in gorilla (Beynon et al., 1991); and around 0.3 years in humans (Gustafson and Koch, 1974). A minimal value of 0.3 year delay in mineralization was used for I<sub>1</sub> and I<sup>1</sup> in Stw 151. The RI<sub>1</sub> root is 8,800 µm long, and would have formed in 392, 426, 459 or 493 days, on periodicities of 7, 8, 9 or 10 days respectively. These represent daily root extension rates of 22, 21, 19 or 18 µm, which are much greater than reported values of 11.7 µm/day in modern gorilla I<sup>1</sup> and I<sub>1</sub> (Beynon et al., 1991); and calculated values of 11.1 and 7.7 µm/day in incisors in a "robust" australopithecine (SK 63) (Dean et al., 1993). Similarly the M<sub>1</sub> with a root 11,900 µm long would have formed in 493, 563, 633 and 703 days, giving extension rates of 24, 21, 19 and 17 µm/day, which are improbably high. These various inconsistencies in molar and incisor development strongly suggest that the canine tooth was initiated relatively late in this specimen.

Two alternative estimates of canine delay were used in the final reconstruction, one (A) of 1.25 years, using an 8 day stria periodicity; and another (B) of 1.0 years, combined with a 9 day periodicity (Fig. 15), giving ages at death of 5.2 or 5.3 years.

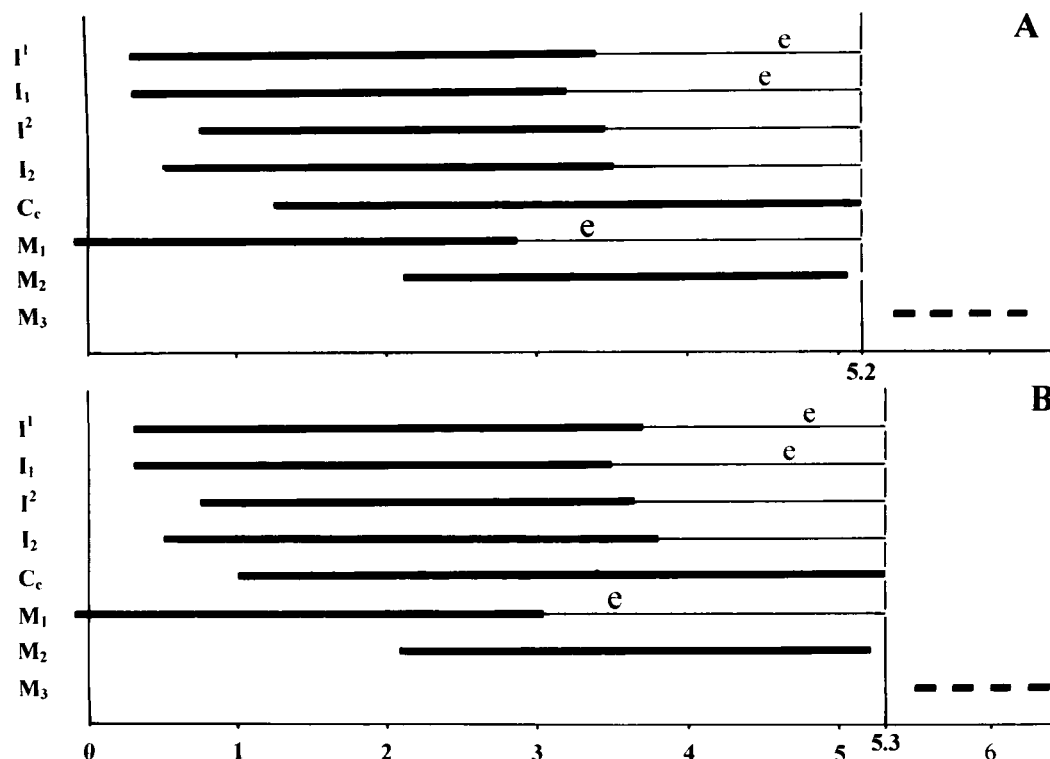


Fig. 15. Bar charts registered using 1.25 year interval (A) or 1.0 year interval (B) between birth and first mineralisation of lower canine; using 8 day (A) or 9 day (B) periodicities between striae; giving estimated ages at death of 5.2 years (A) or 5.3 years (B).

The  $M_1$  was assumed to mineralize 0.1 years before birth, and the 8 and 9 day periodicity values, of 2.95 and 3.13 years, were introduced. The  $M_2$  crown values, summed with 0.1 year, were added, as in the provisional reconstruction. This resulted in 25% (A) and 30% (B) overlap between  $M_1$  and  $M_2$  crown development.

Values for  $I_1$ ,  $I^1$ ,  $I_2$  and  $I^2$  on 8 and 9 day periodicities (Table 5) were used (Fig. 15). The  $I_1$  and  $I^1$  were estimated to mineralize 0.3 years after birth, and crown completion times of 3.2 (A), or 3.5 (B) years for  $I_1$ ; and 3.4 or 3.7 years for  $I^1$  (Table 5) were inserted on the bar chart. Lateral incisors mineralize later than centrals, particularly the  $I^2$ , which begins at 0.9 years in humans (Gustafson and Koch, 1974), and 0.7 years in apes (Winkler, 1995). Postnatal mineralization delay estimates were for  $I_2$  0.5 years, and for  $I^2$  0.75 years (Table 5). The incisor and  $M_1$  root lengths were known, and it was possible

to calculate root extension rates in  $\mu\text{m}/\text{day}$  (Table 6), which ranged from 15.1 to 16.8 in  $I^1$ , from 8.9 to 9.1 in  $I^2$ , and from 14.0 to 14.2 in  $M_1$ . These data match well with the root extension rates of 9 to 15  $\mu\text{m}/\text{day}$  reported by Dean (1995) for selected teeth of the *H. habilis* specimen OH 16. On the basis of this reconstruction the estimated age at death of 5.2 or 5.3 years seems to be more plausible.

It is possible also to derive estimates for age at eruption of  $M_1$  and  $I_1$  using evidence from tooth wear. The differential wear between  $M_1$  and  $I_1$  is considerable, with distinct occlusal and interproximal facets on the  $M_1$  (Fig. 13), which contrasts with the slight abrasion on labial enamel and small interproximal wear facets on  $I_1$ . This suggests that the  $M_1$  had erupted earlier, and had been in functional occlusion for appreciably longer than  $I_1$ . In both modern humans (Gustafson and Koch, 1974) and great apes (Beynon et al., 1991), the  $M_1$  is crown com-

TABLE 5. *Perikymata counts, imbricational and appositional enamel formation times using 7, 8, 9 (and 10) day periodicities between striae, to calculate crown formation times*

|                           | R <sub>C</sub>       | R and LI <sub>1</sub> | LI <sup>1</sup> | RI <sub>2</sub> | RI <sup>2</sup> |
|---------------------------|----------------------|-----------------------|-----------------|-----------------|-----------------|
| Perikymata                | 140                  | 103                   | 111             | 108             | 92              |
| Imbricational enamel (yr) | 2.7, 3.1, 3.5, (3.8) | 2.0, 2.3, 2.5, (2.8)  | 2.1, 2.4, 2.7   | 2.1, 2.4, 2.7   | 1.8, 2.0, 2.3   |
| Appositional enamel (yr)  | 0.8                  | 0.65                  | 0.65            | 0.65            | 0.65            |
| Crown formation time (yr) | 3.5, 3.9, 4.3, (4.6) | 2.6, 2.9, 3.2, (3.5)  | 2.8, 3.1, 3.4   | 2.7, 3.0, 3.3   | 2.4, 2.7, 2.9   |
| Postnatal delay           | 0.5                  | 0.3                   | 0.3             | 0.5             | 0.75            |
| Age at crown completion   | 4.0, 4.4, 4.8, (5.1) | 2.9, 3.2, 3.5, (3.8)  | 3.1, 3.4, 3.7   | 3.2, 3.5, 3.8   | 3.2, 3.4, 3.7   |

These values are summed with estimates of delay from birth to first mineralisation to obtain age at crown completion.

TABLE 6. *Maximum root length in  $\mu\text{m}$ , calculated root formation times (RFT) in days, and root extension rates (RER) in  $\mu\text{m}/\text{day}$* 

|             | M <sub>1</sub> | I <sub>1</sub> | I <sup>1</sup> | I <sub>2</sub> | I <sup>2</sup> |
|-------------|----------------|----------------|----------------|----------------|----------------|
| Root length | 11900          | 8800           | 9800           | 6000           | 5500           |
| RFT A.      | 840            | 712            | 648            | 602            | 621            |
| RFT B.      | 849            | 657            | 584            | 548            | 602            |
| RER A.      | 14.2           | 12.4           | 15.1           | 10.0           | 8.9            |
| RER B.      | 14.0           | 13.4           | 16.8           | 11.0           | 9.1            |

A. Age at death 5.2 years (Fig. 6A), using 8 day stria periodicity, and 1.25 year C<sub>C</sub> delay from birth to first mineralisation. B. Age at death 5.3 years (Fig. 6B), using 9 day stria periodicity, and 1.0 year C<sub>C</sub> delay.

plete at around 3.0 years. In apes the M<sub>1</sub> erupts quickly, 0.5 years after crown completion, but it is delayed by up to 3.5 years in humans.

In Stw 151 the M<sub>1</sub> was estimated to have erupted 0.5 years after crown completion, similar to the delay observed in great apes. In reconstruction A, the M<sub>1</sub> erupted at 3.4 years, 1.8 years before death; in reconstruction B it erupted at 3.5 years, 1.8 years before death. Apart from the deciduous teeth and the first permanent molars, only the central incisors have erupted, but they have not been in occlusion for as long a period as the M<sub>1</sub>, as judged by the limited amount of root development, and lesser occlusal wear. Eruption of the central incisors is estimated at 0.5 years before death, at 4.7 (A) and 4.8 (B) years.

In a recent re-evaluation of cranial capacity and age of M<sub>1</sub> eruption, Smith et al. (1995) have predicted M<sub>1</sub> eruption in *A. africanus* at 3.1 years using a generalised anthropoid equation, and at 3.4 years using a model corrected for chimpanzee residuals. These predicted values are consistent with the values used in this reconstruction.

It is notoriously difficult to make estimates of rates of tooth wear, which depend upon multiple factors including masticatory

function, bite force and abrasivity of the diet (reviewed in Wolpoff, 1971). Occlusal wear is markedly influenced by the presence of foreign material ingested with food. Interproximal wear is less influenced by extraneous material in the diet, depending upon relative movements in two dimensions between adjacent teeth, subjected to a mesial force vector. Wolpoff (1971) made estimates of rates of interproximal wear in modern humans, chimpanzee and australopithecines using published data for development and eruption in the living taxa, and the model proposed by Mann (1968) for australopithecines, based on modern human developmental rates. He found annual rates of wear (in mm) in M<sub>1</sub> of 0.18 in Australian aborigines, 0.23 in chimpanzee, and only 0.13 in australopithecines although this figure would be increased if they followed an apelike developmental chronology.

The loss of 0.5 mm of enamel depth on the M<sub>1</sub> in Stw 151 apparently occurred in less than 1.8 years, suggesting an annual rate of wear of 0.28 mm, which is higher than these estimates. It is possible that wear rates are faster in the beginning, slowing as the facets become larger. These values do suggest however that the rate of interproximal wear is relatively fast in australopithecines, particularly in the early stages. There is marked differential wear on the deciduous molars, with considerable wear on the dm<sub>1</sub> and relatively slight wear on the dm<sub>2</sub>. The finding of modest wear on the dm<sub>2</sub>, in an individual with vigorous masticatory function, lends further support to the proposal that the M<sub>1</sub> erupted early in Stw 151. The slight wear on the labial surface of I<sub>1</sub> is consistent with an occlusal contact period of 0.5 year (or less before full contact is attained) with I<sup>1</sup>. The presence of small mesial interproxi-

mal facets between the  $I_1$  teeth which appear to have formed in a short period gives further support to the suggestion of vigorous masticatory function in this individual. Hinton (1981) has shown that high rates of interproximal wear are associated with powerful and sustained chewing necessary to masticate diets of unprepared seeds, wild plants and small animals. The presence of vertical striations on the labial surface of  $LI_1$  may have represented vertical stripping of abrasive material between clenched teeth in vivo.

### RECONSTRUCTIONS

In order to obtain a more accurate picture of the developmental phases of the dentition of this individual, one of us (JMC) made reconstructions of the maxillary and mandibular arcades from casts of the individual parts. Finally casts of the completed reconstructions were made (Fig. 16).

The presence of the right mandibular body with deciduous molars and the first permanent molar permitted the left side of the mandibular tooth row to be reconstructed by mirror imaging and proper alignment of the teeth. In a similar way, the presence of the left maxillary fragment (though slightly distorted post mortem), with deciduous molars and the impression of the position of the permanent molar and deciduous canine, permitted the reconstruction of the right maxillary tooth row. The areas of resorption on the roots of the deciduous teeth were used as guides to the position of the developing crowns of the succeeding permanent teeth. The widths of the maxillary and mandibular dental arcades were determined with the help of the maxilla and the mandible of the Taung child as guidelines. This specimen was utilized, first, because the Taung child has complete, undistorted, maxillary and mandibular dental arcades and, second, because it is at a developmental stage not very different from, albeit slightly younger than, Stw 151. The use of the Taung specimen as an analogue allowed an approximate matching of the maxilla of the Taung child with the mandible of Stw 151 and of the maxilla of Stw 151 with the Taung mandible. The positions of the anterior teeth were deter-

mined by comparison with the form, curvature and width of the arches of the Taung child. The incisal margins of the maxillary and mandibular central incisors were positioned allowing for the presence of a slight overbite as evidenced by the wear facets.

In the reconstructions, the simultaneous presence of deciduous and permanent teeth in their relative positions, and the relative positions of the developing permanent teeth, allow us to observe the sequence of development of the permanent teeth. Such a sequence may be observed in the maxilla, for the  $LP^3$  and  $L^C$ , relative to the  $Ldm^1$  (even though the canine must have been slightly displaced post mortem because it is positioned very close to the median plane), and for the  $LP^3$  to the  $L^C$ . In the mandible the crown of the  $RP_4$  is exposed in its crypt, while the  $R_C$  is also lying in its natural position close to the inferior margin of the body of the mandible. A single piece preserves the  $LI_2$  and  $L_C$  in their relative developmental position without any apparent distortion.

The mandibular incisors are moderately crowded. To a lesser extent this is evident also in the maxillary incisors. (The  $RI^2$  has probably been displaced post mortem, as is suggested by its unusual position in the maxilla.) Such crowding of the developing teeth is often observed in modern human subjects (DuBrul, 1980), as well in some early hominid specimens (Dean, 1987). It is considered to be due to a disproportion between the size of the teeth and of the space in the developing jaw. When more space becomes available, following the growth of the jaw, the teeth may adjust their position into proper alignment. Similarly, the developing crowns of the  $RP_3$  and  $RP_4$  are rotated in their crypts. This is shown for the  $RP_3$ , from an X-ray image, while for the  $RP_4$  it can be observed directly. The first mandibular molars are obliquely placed, that is with their occlusal surfaces slightly tilted lingually. This condition produced the particular orientation of the wear facets which can be observed on the main cusps.

The presence of an overbite in some juvenile individuals of Australopithecinae with developing dentition has been noted by Wallace (1978), who observes that in *A. robustus*

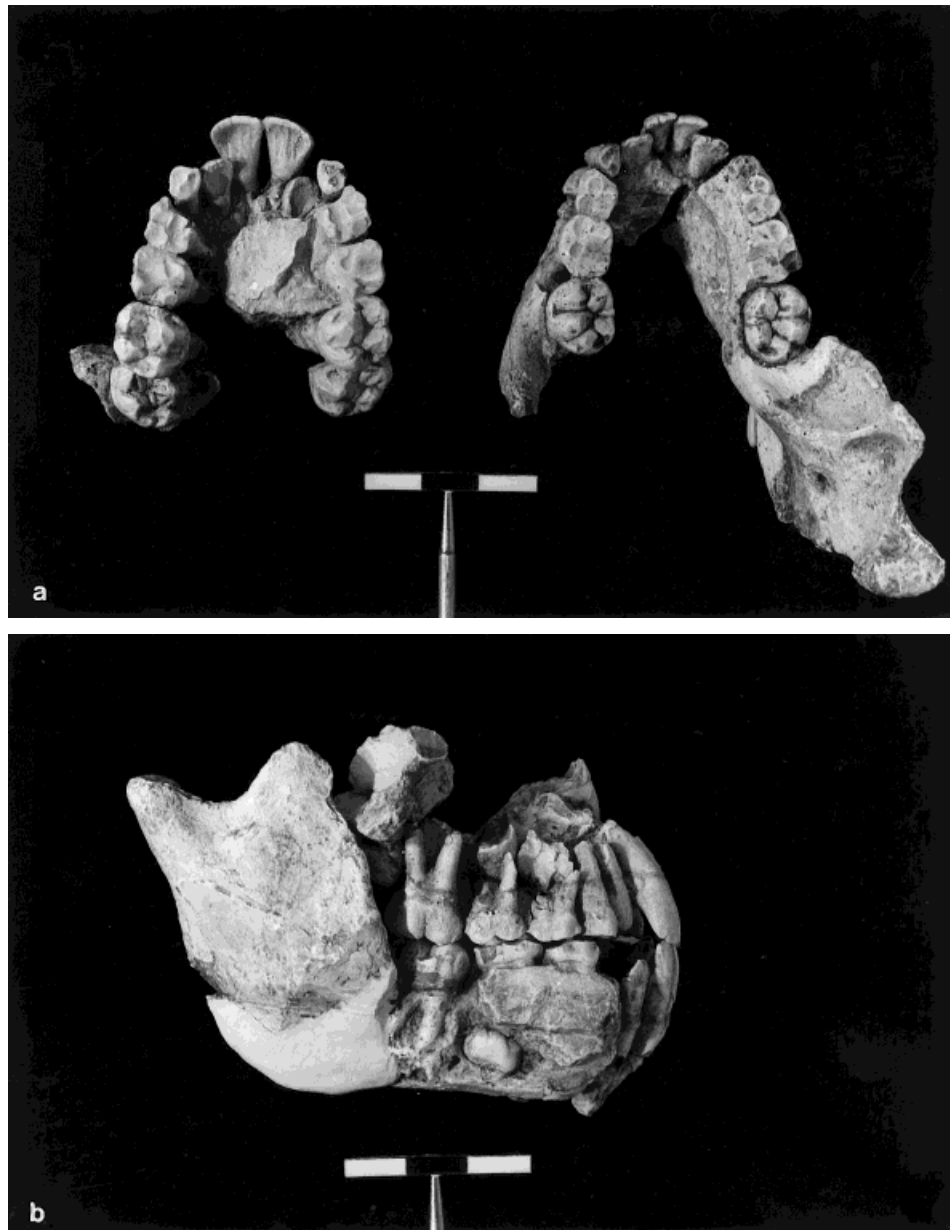


Fig. 16. **a:** Reconstruction of the maxilla and the mandible of Stw 151. **b:** The two reconstructed parts in occlusion.

an edge-to-edge contact between maxillary and mandibular incisors developed earlier in life than in *A. africanus*. He related this to a difference in the position of eruption of the incisors. In *A. robustus*, he inferred, an orthognathous maxilla determines the almost vertical eruption of the incisors, lead-

ing to an early edge-to-edge contact between maxillary and mandibular incisors. In *A. africanus*, on the other hand, the maxillary incisors developed in a prognathous maxilla, thus erupting obliquely downward and forward. This resulted in an upward and inward inclination of the attrition plane, which



can be observed in some *A. africanus* specimens (e.g. Sts 52a-52b).

Thus, the pattern of attrition of the incisors of Stw 151 is in keeping with that which characterizes *A. africanus*.

## DISCUSSION AND CONCLUSIONS

The remarkable number of teeth present in the mixed dentition of this juvenile individual (together with the associated cranial fragments) and the comparison with some other early hominids from South (and East) Africa, enabled some conclusions to be drawn on the systematic position of this specimen and also some inferences to be made relative to the dental development of early hominids.

### Systematic affinities

The analysis of the morphological traits of the teeth of Stw 151 shows a number of traits that traditionally have been described as typical of *A. africanus* (Robinson, 1956; Grine 1984) and it lacks, overall, features present in *A. robustus*. The metrical analysis of the dentition provides similar results. Each tooth measurement falls in the lower part of the range of distribution for *A. africanus* or, in some cases, outside of it.

Thus, the morphology and metrics of the teeth clearly separate Stw 151 from *A. robustus* and closely ally it with the *A. africanus* sample as presently known.

At the same time, however, some affinities with early *Homo* are also present, and these are to be found specifically in those features which are considered by most authors to be more systematically relevant in the diagnosis of the genus *Homo*, namely BL reduction and MD elongation of M<sub>1</sub>, and MD elongation of M<sup>1</sup> (Tobias, 1991; Suwa et al., 1996).

In respect of the pattern of attrition of the front teeth of Stw 151, the evidence suggests a stronger similarity with that of *A. africanus* than with that of *A. robustus*.

The comparison of the associated skull fragments of Stw 151 with other juvenile specimens of fossil hominids provides other relevant information. The morphological features of the mandible of Stw 151 indicate major differences with *A. robustus*, as represented by SK 63, and overall similarities with the Taung child, adding evidence to the distinctiveness of Stw 151 from *A. robustus*.

Differences between Stw 151 and the Taung child (and the *A. afarensis* juvenile AL 333-105) are evident mainly in the glenoid region, especially in the different development of the entoglenoid process relative to the temporal spine. The condition as observed in the two juvenile specimens (Taung and AL 333-105) seems to be comparable to the adult condition of *Australopithecus* as described by Tobias (1991), indicating no difference, in this respect, between the juvenile and the adult condition. On this ground, the similarities between Stw 151 and adult specimens of *H. habilis* seem to suggest that, for this character, Stw 151 shows a condition more derived towards early *Homo* than that of Taung and AL 333-105.

The other features that can be compared in Stw 151 and the Taung child show differences between the juvenile and the adult condition, and, as such, are of no use in the assessment of the systematic position.

Relevant comparisons of Stw 151 with adult skull morphology have to be limited to the analysis of the orientation of the posterior surface of the petrous bone, because of the reported lack of (or minor) difference from an adult condition (Spoor, 1993). Both the morphological analysis and the metrical study published by Spoor (1993) provide additional and independent evidence of difference in this character between Stw 151 and the *A. africanus* sample, and similarity with early *Homo*.

In the same study, Spoor (1993) considered also a number of features of the morphology of the bony labyrinth in Stw 151 and several other South African hominids. He was able, for example, to assess quantitatively the coronal orientation of the posterior petrosal surface, showing similarities with a human-like condition. In his analysis he concluded that "it is feasible that Stw 158 [Stw 151] is affiliated with a more derived form of hominid than *A. africanus*" (Spoor, 1993).

The combined information of the dentition and other cranial fragments provides discordant evidence. The teeth show overall affinities with *A. africanus* (but also differences in some key traits), whereas the cranial pieces present a few features more derived towards an early *Homo* condition. The picture emerg-

ing is that of a specimen with a dentition not fully distinct from that of *A. africanus*, but with a cranial morphology more derived in some characters.

An additional factor to be considered in the interpretation of this morphological evidence is the stratigraphical position of the specimen within the Sterkfontein deposit. Stw 151 derives from the southern part of the deposit, with no stone tools associated, and from a relatively shallow dept, in an area which probably forms part of the Member 4 breccia deposit considered by Kuman and Clarke (in press) to represent a later phase of deposition with respect to the bulk of Member 4.

Thus, on the basis of the combined morphological evidence, together with the information on its stratigraphic provenance, the possibility that Stw 151 may represent a slightly later hominid, which in some respect is more derived towards an early *Homo* condition than the rest of the *A. africanus* sample from Member 4, has to be taken into consideration.

Several studies have suggested that, while the overwhelming majority of specimens from Sterkfontein Member 4 are assignable to the species *A. africanus*, a small handful of specimens seem to be difficult to accommodate in that species and may represent another taxon (Clarke, 1988; Kimbel and White, 1988; Kimbel and Rak, 1993; Calcagno et al., 1997; Lockwood, 1997).

According to Clarke (1988) the variation observed in the Member 4 sample represents two species: one (*A. africanus*), with smaller teeth, ancestral to *Homo*; and the other, with larger teeth, ancestral to *A. robustus*, although he did not show statistically significant differences between his proposed two subsets. Kimbel and White (1988) have pointed out that the variability in dental dimensions and in some features of the cranial base cannot be attributed to sexual dimorphism; they have hypothesised the presence in the Member 4 deposit of temporally mixed samples and/or of more than one hominid species. Subsequently, Kimbel and Rak (1993) have, more specifically, assigned Sts 19 (a cranial base from Member 4) to early *Homo*. More recently, Calcagno et al. (1997) on dental measure-

ments and Lockwood (1997) on facial morphology have supported the possibility that not all of the specimens purported to have emanated from Member 4 necessarily represent the same species.

At the same time, other authors—for example Suwa (1990) in his study of premolar morphology and Wood (1991b) in his analysis of the metrical variability of the dentition of *A. africanus*—could find no evidence against the substantial systematic homogeneity within the Sterkfontein Member 4 hominid sample.

Within this framework, our analysis of Stw 151, seems to provide some support for the presence of a second taxon, at least within the supposedly latest part of Member 4 deposits.

At the same time, it highlights the importance of integrating, where possible, different sets of data, including stratigraphical evidence, in the systematic interpretation of fossil specimens. Moreover, it suggests that systematic inferences based on the analysis of the dentition alone must be considered cautiously.

#### Dental development

The completeness and preservation (including microstructural features) of the permanent teeth of Stw 151 allowed us to obtain some specific information about the relative dental development of this specimen.

The detailed histological study allowed us to test directly the provisional developmental model proposed by Beynon and Dean (1988) on a juvenile “gracile” australopithecine individual, and it appears to confirm the rapid maturation rate of the teeth of these fossil hominids. This study also showed major differences in the dental development of “gracile” australopithecines from *A. robustus*, for example in the increasing density of perikymata in the cervical portion of the tooth crowns, and in the number of perikymata on the lower central incisors (Stw 151,  $n = 103$ ; *A. robustus* range = 57–86, Beynon and Dean, 1988). This indicated that incisor crowns formed over a slightly longer period of time in Stw 151 as compared to *A. robustus*.

In terms of developmental sequence, Stw 151 shows a number of interesting features: 1) the late development of incisors relative to M1; 2) the suggested late initiation of mineralization of the canine tooth; 3) the slow development of the molar tooth series, with the M2 being only crown complete when the M1 roots are nearly complete, and the M3 crown apparently being at the earliest stage of its mineralization.

These features, as a whole, point to differences in the dental developmental sequence from both chimpanzees (because of the slow development of the molar tooth series) and humans (because of the late development of incisors relative to first molars). This reinforces the notion that the dental developmental patterns of fossil hominids are distinctive.

The estimated age at death of 5.2 or 5.3 years for Stw 151 seems also to differ from both humans and chimpanzees at a similar stage of development of the first molars (Fig. 17). On a human scale (following Schour and Massler, 1941, adapted by Berkovitz et al., 1992), the inferred age of Stw 151 would be 8 years ( $\pm 9$  months), whereas on a chimpanzee scale (following Chandrasekera et al., 1993), it would be approximately 6 years. An age at death of 5.2–5.3 years is consistent with an earlier estimate of 5 years proposed by Smith (1989).

More relevant information may be obtained by a comparison of the developmental sequence of this specimen with known *A. africanus* specimens. A careful interpretation of the dental developmental pattern of a single fossil juvenile individual requires that it be examined together with other juvenile specimens of similar developmental age (see Conroy and Kuykendall, 1995, for example). A detailed comparison of this kind, however, is difficult since there are no juvenile specimens of *A. africanus* with the dentition at a similar developmental stage as Stw 151: both Taung and Sts 24 are younger than Stw 151, in having the roots of M1 completed for more than half of their length, but none of them having any incisor roots formed. Stw 151 has erupted first molars, with nearly complete roots, and crowns which have been in functional occlusion for an extended period, to judge by the occlusal and interproximal

wear. The central incisors had only recently come into functional occlusion (as evidenced by the relatively modest wear), with  $\frac{1}{2}$  to  $\frac{3}{4}$  root completion, and the lateral incisors have not yet erupted.

Delayed development of I1 relative to M1, as evident in the Taung child and in Sts 24, is typical of *A. africanus*. This is evident in Stw 151, although the extent of the difference in the development of the two teeth is not so marked as in Taung and Sts 24. The reduction in the gap between the different developmental phases of the I1 and of the M1 may thus be related to a relatively faster developmental rate of the incisor roots after tooth eruption, allowing these teeth to “catch-up” with the development of the first molars. Differences in the developmental sequences of the two teeth seem to be more marked at younger ages, becoming less evident at older ages. Furthermore, it cannot be assumed that, from a sample of only two individuals, Sts 24 and Taung, we have gauged adequately the extent of the differences in the development of the two teeth. In that light, Stw 151 may simply be extending the known range of differences in the developmental sequences.

Stw 151 is at a later stage of development than these two specimens, with M1 roots complete, and incisor roots ranging from  $\frac{1}{3}$  (RI<sub>2</sub>) to  $\frac{3}{4}$  (L and RI<sub>1</sub>) complete. The chronology of dental development proposed for this specimen can be used to estimate the age at death for these younger specimens. The Taung child with incomplete M1 roots, and incisor and canine crowns at the stage of crown completion, would have been around 3.5 years, which value is consistent with earlier estimates proposed by Conroy and Vannier (1987, 1991b). Sts 24, with incisor root formation commencing, is consistent with an age around 3.5–4.0 years (Conroy and Vannier, 1991b).

A comparison of Stw 151 with a fossil specimen in a similar developmental stage of the M1, KNM-ER 1590 (an East African early *Homo*), reveals a condition slightly different in the development of I<sup>1</sup> relative to M<sup>1</sup>. In this case the roots of the I<sup>1</sup> are almost complete and, at the same time, the roots of the premolars show more advanced development than those of Stw 151.

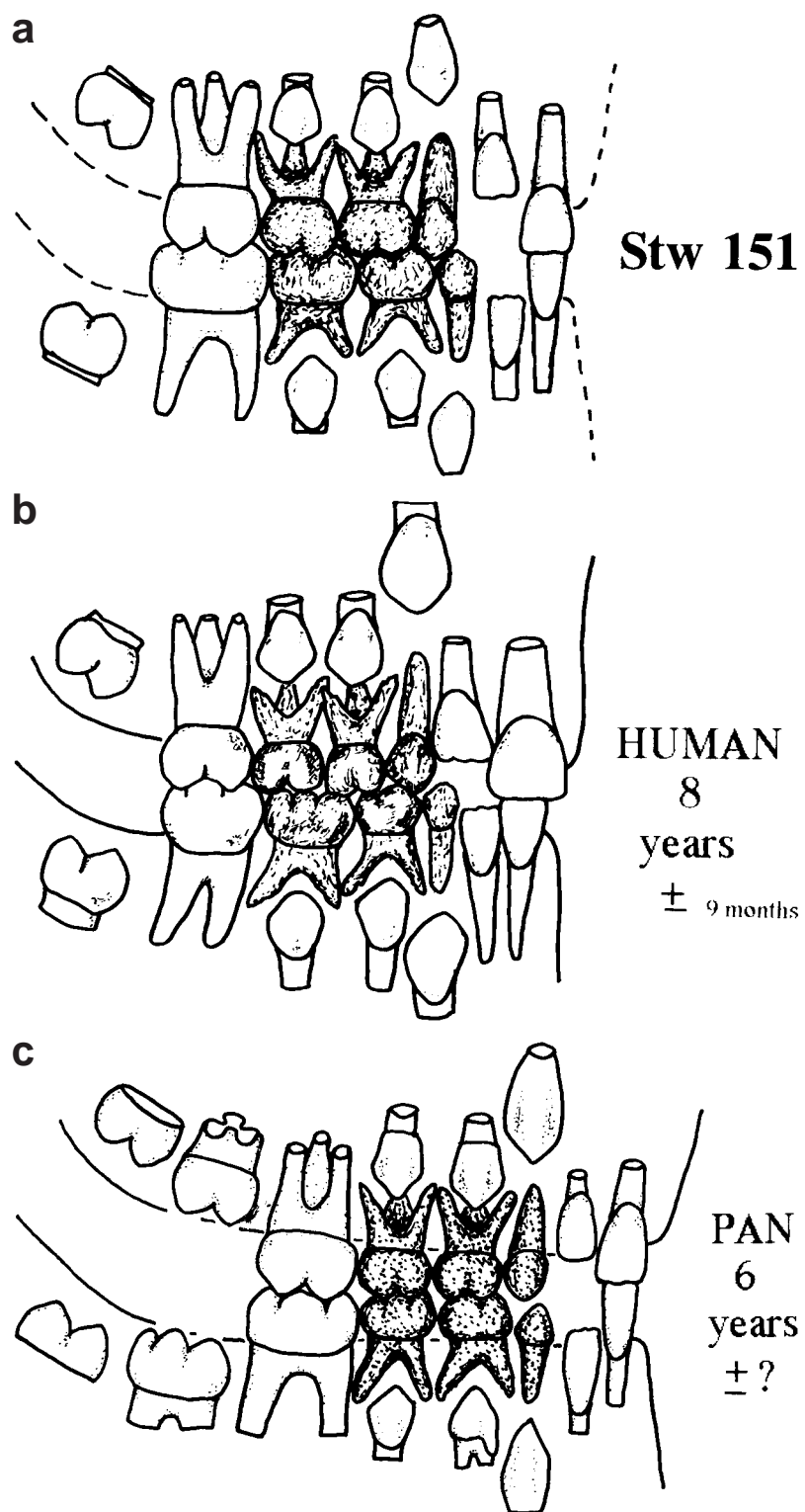


Fig. 17. Dental developmental stages of Stw 151 (a) compared with humans (b) and chimpanzees (c) of equivalent stage of development of M1. Human scale following Schour and Massler (1941), adapted by Berkovitz et al. (1992). Chimpanzee scale following Chandrasekera et al. (1993).

Another East African early *Homo* juvenile specimen with developing dentition is KNM-ER 820 (Dean, 1987). This mandible has similar  $M_1/M_2$  developmental relationships to Stw 151, but has erupted  $I_1$  and  $I_2$ . Both incisors have undergone some wear, exposing the underlying incisal dentine in the  $I_1$ , suggesting that these teeth had erupted earlier in this specimen, closer to the  $M_1$ . This would appear to represent a significant difference between *A. africanus* and later *Homo* taxa.

Thus, Stw 151 seems to show more similarities to an *A. africanus* sequence of dental development, the only difference from Taung and Sts 24 being due to the older age of the specimen.

The analysis of these three specimens of South African hominids indicates that variability has to be taken into account when studying the dental developmental patterns of fossil hominids. In this respect, a recent attempt to study the variability in the dental developmental patterns of *A. africanus* (including Stw 151) has been carried out (Moggi-Cecchi, 1997, 1998) using an age-independent method of analysis proposed by Smith (1994). For this kind of analysis six fairly complete specimens of *A. africanus*, of different developmental age, have been included, namely Taung, MLD 2, MLD 11/30, Sts 24, Stw 183, Stw 412 plus Stw 151. On this approach, the dental developmental pattern of Stw 151 does not seem to differ much from those of *A. africanus* specimens.

This study confirmed some of the similarities of the dental developmental patterns of *A. africanus* with developmental patterns of living african apes, as already described by other authors (Smith, 1994; Beynon and Dean, 1988; Conroy and Kuykendall, 1995), but at the same time it revealed notable differences. Also, it confirmed that the range of variability of the dental developmental patterns of *A. africanus* only partially overlaps that of modern humans, indicating that dental developmental patterns of *A. africanus* cannot all be accommodated within those of modern humans. These results confirm the need to abandon the use of such terms as "more ape-like" or "more human-like," when one studies the dental developmental patterns of fossil hominids.

## Conclusions

In this study it has been possible to combine complementary sets of information on the juvenile fossil hominid Stw 151, namely the analysis of the morphological and metrical features of the dentition, the study of associated skull fragments, and the micro-anatomical examination of the developing permanent teeth, in terms of both pattern and chronology.

1. The analysis of the dentition together with that of the glenoid region and of the petrous bone raise the possibility that Stw 151 be considered to represent a hominid taxon that is more derived towards an early *Homo* condition than the rest of the *A. africanus* sample from Member 4.

2. The features of the developing dentition show differences from both modern humans and apes, reinforcing the notion of the distinctiveness of the dental developmental patterns of fossil hominids.

3. The developmental pattern observed in the dentition of Stw 151 accords with the pattern ascribed to *A. africanus*.

4. On the basis of the microanatomical study of the developing dentition the inferred age at death of Stw 151 is 5.2 to 5.3 years.

## ACKNOWLEDGMENTS

We thank many scholars, who at different times discussed with us some issues related to the juvenile individual Stw 151, notably Drs. L.R. Berger, T.G. Bromage, G.C. Conroy, F.E. Grine, K. Kuykendall, A.E. Mann, G.H. Sperber; special thanks are due to Dr. C.A. Lockwood, for careful revision of the manuscript and numerous suggestions, Dr. M.C. Dean, for his contribution to the reconstructions and valuable suggestions, Dr. R.J. Clarke for discussion and comments, Dr. K. Kuman for sharing her information on the new interpretation of the stratigraphy at Sterkfontein, Mr. P.S. Quinney and Mr. P. Faugust for technical help. Our appreciation is extended to Dr. C.K. Brain and Dr. F. Thackeray for allowing us access to specimens housed in the Transvaal Museum, Pretoria. We dedicate this paper to the late Mr. A.R. Hughes, who first encouraged JMC to assemble the different parts of Stw 151 in



a reconstruction and provided useful information on the stratigraphic provenance of the different parts of Stw 151. The research was carried out with a grant from the Italian Consiglio Nazionale delle Ricerche (AI 93.00547.04) and a postdoctoral fellowship from the South African Foundation for Research and Development to JMC.

## LITERATURE CITED

- Anemone RL, Mooney MP, and Siegel MI (1996) Longitudinal study of dental development in chimpanzees of known chronological age: Implications for understanding the age at death of Plio-Pleistocene hominids. *Am. J. Phys. Anthropol.* 99:119–134.
- Berger LR (1994) Functional morphology of the hominoid shoulder, past and present. PhD thesis, Johannesburg, University of the Witwatersrand.
- Berkovitz BKB, Holland GR, and Moxham B (1992) A Colour Atlas and Text of Oral Anatomy, Histology and Embryology, 2nd ed. London: Wolfe.
- Beynon AD (1987) Replication techniques for studying microstructure in fossil enamel. *Scanning Microsc.* 1:663–669.
- Beynon AD (1992) Circaseptan rhythms in enamel development in modern humans and Plio-Pleistocene hominids. In P Smith and E Tchernov (eds): *Structure, Function and Evolution of Teeth*. London, Tel Aviv: Freund Publishing, pp. 295–309.
- Beynon AD and Dean MC (1988) Distinct dental development patterns in early fossil hominid. *Nature* 335:509–514.
- Beynon AD and Dean MC (1991) Hominid dental development. *Nature* 351:196.
- Beynon AD, Dean MC, and Reid DJ (1991) Histological study on the chronology of the developing dentition in gorilla and orangutan. *Am. J. Phys. Anthropol.* 86:189–203.
- Bromage TG (1985) Taung facial remodeling: A growth and development study. In Tobias PV (ed): *Hominid Evolution: Past, Present and Future*. New York: Alan R. Liss, pp. 239–245.
- Bromage TG and Dean MC (1985) Re-evaluation of age at death of immature fossil hominids. *Nature* 317:525–527.
- Bromage TG, Schrenk F, and Zonneveld FW (1995) Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *J. Hum. Evol.* 28:71–108.
- Calcagno JM, Cope DA, Lacy MG, and Tobias PV (1997) Is *A. africanus* the only hominid species in Sterkfontein Member 4? *Am. J. Phys. Anthropol.* (suppl.) 24:86–87.
- Chandrasekera MS, Reid DJ, and Beynon AD (1993) Dental chronology in chimpanzee (*Pan troglodytes*) *J. Dent. Res.* 72:729.
- Clarke RJ (1977) The cranium of the Swartkrans hominid, SK 847 and its relevance to human origins. PhD thesis, Johannesburg, University of the Witwatersrand.
- Clarke RJ (1988) A new *Australopithecus* cranium from Sterkfontein and its bearing on the ancestry of *Paranthropus*. In Grine FE (ed): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 285–292.
- Clarke RJ (1994) On some new interpretations of Sterkfontein stratigraphy. *S. Afr. J. Sci.* 90:211–214.
- Conroy GC and Kuykendall K (1995) Paleopediatrics: Or when did human infants really become human? *Am. J. Phys. Anthropol.* 98:121–131.
- Conroy GC and Vannier MW (1987) Dental development of the Taung skull from computerized tomography. *Nature* 329:625–627.
- Conroy GC and Vannier MW (1991a) Dental development in South African Australopithecines. Part I: Problems of pattern and chronology. *Am. J. Phys. Anthropol.* 86:121–136.
- Conroy GC and Vannier MW (1991b) Dental development in South African Australopithecines. Part II: Dental stage assessment. *Am. J. Phys. Anthropol.* 86:137–156.
- Dean MC (1987) The dental developmental status of six East African juvenile fossil hominids. *J. Hum. Evol.* 16:197–213.
- Dean MC (1995) The nature and periodicity of incremental lines in primate dentine and their relationship to periradicular bands in OH 16 (*Homo habilis*). In J Moggi-Cecchi (ed): *Aspects of Dental Biology: Palaeontology, Anthropology and Evolution*. Florence: International Institute for the Study of Man, pp. 239–266.
- Dean MC, Beynon AD, Thackeray JF, and Macho GA (1993) Histological reconstruction of dental development and age at death of a juvenile *Paranthropus robustus* specimen, SK 63, from Swartkrans, South Africa. *Am. J. Phys. Anthropol.* 91:401–419.
- DuBrul LL (1980) *Sicher's Oral Anatomy*. St. Louis: Mosby.
- Enlow DH (1982) *A Handbook of Facial Growth*, 2nd ed. Philadelphia: Saunders, 486 pp.
- Fanning EA and Moorrees CFA (1969) A comparison of permanent mandibular molar formation in Australian aborigines and caucasoids. *Arch. Oral. Biol.* 14:999–1006.
- Fitzgerald C (1996) Tooth crown formation and the variation of enamel microstructural growth markers in modern humans. Ph.D thesis, University of Cambridge.
- Fleagle JG (1988) *Primate Adaptation and Evolution*. San Diego: Academic Press.
- Grine FE (1984) The deciduous dentition of the Kalahari San, the South African Negro and the South African Plio-Pleistocene Hominids. PhD thesis, Johannesburg, University of the Witwatersrand.
- Grine FE (1985) Australopithecine evolution: the deciduous dental evidence. In E Delson (ed): *Ancestors: The Hard Evidence*. New York: Alan R. Liss, pp. 153–167.
- Grine FE (1986) Anthropological aspects of the deciduous teeth of South African blacks. In R Singer and JK Lundy (eds): *Variation, Culture and Evolution in African Populations*. Johannesburg, Witwatersrand University Press, pp. 47–83.
- Gustafson G and Koch G (1974) Age estimation up to 16 years of age based on dental development. *Odont. Revy* 25:297–306.
- Hinton RJ (1981) Form and patterning of anterior tooth wear among aboriginal human groups. *Am. J. Phys. Anthropol.* 54:555–564.
- Hughes AR and Tobias PV (1977) A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature* 265:310–312.
- Kay RF and Hiiemae KM (1974) Jaw movement and tooth use in recent and fossil primates. *Am. J. Phys. Anthropol.* 40:227–256.
- Kimbel WH and Rak Y (1993) The importance of species taxa in paleoanthropology and an argument for the phylogenetic concept of the species category. In WH Kimbel and LB Martin (eds): *Species, Species Concepts, and Primate evolution*. New York: Plenum, pp. 461–485.

- Kimbel WH and White TD (1988) Variation, sexual dimorphism and the taxonomy of *Australopithecus*. In Grine FE (ed): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 175–192.
- Kimbel WH, Johanson DC, and Coppens Y (1982) Pliocene hominid cranial remains from the Hadar Formation, Ethiopia. *Am. J. Phys. Anthropol.* 57:453–499.
- Kimbel WH, Johanson DC, and Rak Y (1997) Systematic assessment of a maxilla of *Homo* from Hadar, Ethiopia. *Am. J. Phys. Anthropol.* 103:235–262.
- Kuman K (1994a) The archaeology of Sterkfontein: Preliminary findings on site formation and cultural change. *S. Afr. J. Sci.* 90:215–219.
- Kuman K (1994b) The archaeology of Sterkfontein—past and present. *J. Hum. Evol.* 27:471–495.
- Kuman K and Clarke RJ (in press) Stratigraphy, artefact industries and hominid associations from Sterkfontein, Member 5. *J. Hum. Evol.*
- Kuykendall KL (1996) Dental development in chimpanzees (*Pan troglodytes*): The timing of tooth calcification stages. *Am. J. Phys. Anthropol.* 99:135–158.
- Lockwood CA (1997) Variation in the face of *Australopithecus africanus* and other African Hominoids. PhD thesis, Johannesburg, University of the Witwatersrand.
- Logan WHG and Kronfeld R (1933) Development of human jaws and surrounding structures from birth to age of fifteen years. *J. Am. Dent. Assoc.* 20:379–427.
- Mann AE (1968) The paleodemography of *Australopithecus*. PhD thesis, University of California at Berkeley. Ann Arbor, University Microfilms.
- Mann AE (1975) Some Paleodemographic Aspects of the South African Australopithecines. Philadelphia: University of Pennsylvania Press.
- Mann A, Lampl M, and Monge J (1990) Patterns of ontogeny in human evolution: Evidence from dental development. *Yrbk. Phys. Anthropol.* 33:111–150.
- Mann AE, Monge JM, and Lampl M (1991) Investigation into the relationship between perikymata counts and crown formation times. *Am. J. Phys. Anthropol.* 86:175–188.
- Martin R and Knussmann R (1988) *Anthropologie*. Band I/1. Stuttgart: Gustav Fischer Verlag.
- Moggi-Cecchi J (1997) Variability in the patterns of dental development of *Australopithecus africanus*. *J. Hum. Evol.* 32:A14 (abstract).
- Moggi-Cecchi J (1998) Variability in the patterns of dental development of *Australopithecus africanus*: A first approach. In Facchini F, di Cesnola AP, Piperno M, and Peretto C (eds): XIII UISPP Congress 1996 Proceedings. Sections 4–6. Forti: A.B.A.C.O., pp. 43–47.
- Moggi-Cecchi J and Tobias PV (1993) Preliminary note on a new juvenile hominid individual from Sterkfontein Formation, South Africa. *Antropol. Contemp.* 16:213–219.
- Moorrees CFA, Fanning EA, and Hunt EE (1963) Age variation of formation stages for ten permanent teeth. *J. Dent. Res.* 42:1490–1502.
- Partridge TC (1978) Re-appraisal of lithostratigraphy of Sterkfontein hominid site. *Nature* 275:283–287.
- Partridge TC, Tobias PV, and Hughes AR (1991) Paleoeologie et affinités entre les australopithecines d'Afrique du Sud: nouvelles données de Sterkfontein et Taung. *L'Anthropologie* (Paris). 95:363–378.
- Potente F and Moggi-Cecchi J (1995) Video observation and enhancement of tooth wear by electronic filtering. In J Moggi-Cecchi (ed): *Aspects of Dental Biology: Palaeontology, Anthropology and Evolution*. Florence: International Institute for the Study of Man, pp. 167–175.
- Reid DJ, Beynon AD, and Ramirez-Rozzi FV (in press) Histological reconstruction of dental development in four individuals from a medieval site in Picardie, France. *J. Hum. Evol.*
- Robinson JT (1956) The Dentition of the Australopithecinae. Pretoria; Transvaal Museum Memoirs n. 9.
- Schour I and Massler M (1941) The development of the human dentition. *J. Am. Dent. Assoc.* 28:1153–1160.
- Simpson SW, Lovejoy CO, and Meindl RS (1990) Hominoid dental maturation. *J. Hum. Evol.* 19:285–297.
- Simpson SW, Lovejoy CO, and Meindl RS (1991) Relative dental development in Hominoids and its failure to predict somatic growth velocity. *Am. J. Phys. Anthropol.* 86:113–120.
- Smith BH (1986) Dental development in *Australopithecus* and early *Homo*. *Nature* 323:327–330.
- Smith BH (1989) Growth and development and its significance for early hominid behaviour. *OSSA* 14: 63–96.
- Smith BH (1991) Dental development and the evolution of life history in Hominidae. *Am. J. Phys. Anthropol.* 86:157–174.
- Smith BH (1994) Patterns of dental development in *Homo*, *Australopithecus*, *Pan* and *Gorilla*. *Am. J. Phys. Anthropol.* 94:307–325.
- Smith RJ, Gannon PJ, and Smith BH (1995) Ontogeny of australopithecines and early *Homo*: Evidence from cranial capacity and dental eruption. *J. Hum. Evol.* 29:155–168.
- Sperber GH (1973) Morphology of the cheek teeth of early South African Hominids. PhD thesis, Johannesburg, University of the Witwatersrand.
- Spoor CF (1993) The comparative morphology and phylogeny of the human bony labyrinth. Doctoral thesis, Universiteit Utrecht.
- Suwa G (1988) Evolution of the "robust" australopithecines in the Omo succession: Evidence from mandibular premolar morphology. In Grine FE (ed): *Evolutionary History of the "Robust" Australopithecines*. New York: Aldine de Gruyter, pp. 199–222.
- Suwa G (1990) A comparative analysis of hominid dental remains from the Shungura and Usno Formations, Omo valley, Ethiopia. Ann Arbor: UMI.
- Suwa G, White TD, and Howell FC (1996) Mandibular postcanine dentition from the Shungura formation, Ethiopia: Crown morphology, taxonomic allocations, and Plio-Pleistocene hominid evolution. *Am. J. Phys. Anthropol.* 101:247–282.
- Tobias PV (1967) Olduvai Gorge, vol. 2. The Cranium and Maxillary Dentition of *Australopithecus (Zinjanthropus) boisei*. Cambridge: Cambridge University Press.
- Tobias PV (1983) Seventeenth Annual Report of the Palaeo-Anthropology Research Group (September 1982–September 1983). Johannesburg, University of the Witwatersrand, Department of Anatomy and Human Biology.
- Tobias PV (1991) Olduvai Gorge, vols. 4A and 4B. The Skulls, Endocasts and Teeth of *Homo habilis*. Cambridge: Cambridge University Press.
- Tobias PV (1993) Earliest *Homo* not proven. *Nature* 361:307.
- Tobias PV (1994) Palaeo-anthropology in South Africa. *S. Afr. J. Sci.* 90:203–204.
- Tobias PV and Hughes AR (1969) The new Witwatersrand University excavation at Sterkfontein. *S. Afr. Archaeol. Bull.* 24:158–169.

- Ungar PS and Grine FE (1991) Incisor size and wear in *Australopithecus africanus* and *Paranthropus robustus*. *J. Hum. Evol.* 20:313–340.
- Wallace JA (1978) Evolutionary trends in the early hominid dentition. In CJ Jolly (ed): *Early Hominids of Africa*. London: Duckworth, pp. 285–310.
- Weidenreich F (1936) The mandibles of *Sinanthropus pekinensis*: A comparative study. *Palaeontol. Sinica*. n.s. D, 7:1–162.
- Weidenreich F (1943) The skull of *Sinanthropus pekinensis*: A comparative study on a primitive hominid skull. *Palaeontol. Sinica*. n.s. D, 10:1–298.
- White TD and Johanson DC (1982) Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974–1977 collections. *Am. J. Phys. Anthropol.* 57:501–544.
- White TD, Johanson DC, and Kimbel WH (1981) *Australopithecus africanus*: Its phyletic position reconsidered. *S. Afr. J. Sci.* 77:445–470.
- Winkler LA (1995) A comparison of radiographic and anatomical evidence of tooth development in infant apes. *Folia Primatol.* 65:1–13.
- Wolpoff MH (1971) Interstitial wear. *Am. J. Phys. Anthropol.* 34:205–228.
- Wood BA (1991a) Koobi Fora Research Project, vol. 4. *Hominid Cranial Remains*. Oxford: Clarendon.
- Wood BA (1991b) A paleoanthropological model for determining the limits of early hominid taxonomic variability. *Palaeontol. Afr.* 28:71–77.
- Wood BA (1992) Origin and evolution of the genus *Homo*. *Nature* 355:783–790.
- Wood BA (1993) Early *Homo*: How many species? In WH Kimbel and LB Martin (eds): *Species, Species Concepts, and Primate Evolution*. New York: Plenum, pp. 485–522.
- Wood BA and Engleman CA (1988) Analysis of the dental morphology of Plio-Pleistocene hominids. V. Maxillary postcanine tooth morphology. *J. Anat.* 161: 1–35.
- Wood BA and Uytterschaut H (1987) Analysis of the dental morphology of Plio-Pleistocene hominids. III. Mandibular premolar crowns. *J. Anat.* 154:121–156.